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POLLEN MORPHOLOGICAL STUDIES IN THE ACANTHACEAE

BY

BHOJ RAJ

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Introduction

The Acanthaceae is a distinctly eurypalynous family comprising about 220 genera and over 2000 species, mostly growing in the warmer parts of the world.

The first person to be attracted by the pollen grains of Acanthaceae appears to have been F. Bauer (1790-1840). On a fine summer day, during his stay in Kew, he sketched the pollen grains of *Thunbergia alata*.

Detailed investigations of acanthaceous pollen grains were carried out by Fritzsche (1837) and Mohl (1834) and also by Bischoff (1833). According to Fritzsche a classification of pollen forms has just as much right and may be as much natural as the classification of plants themselves. The amount of work done and knowledge amassed, dating from that of Fritzsche (1837), Lindau (1895) and the contributions of Wodehouse and Erdtman, have only proved the truth of Fritzsche's statement.

The taxonomical value of the pollen grain characters in the system of the Acanthaceae was first pointed out by Radlkofer (1883). He distinguished several acanthaceous pollen types and described them as "Furchen-, Waben-, Schalen-, Dosen-, Spangen-, Rahmen-, und Rippenpollen".

Lindau also realized the taxonomical importance of the different pollen types in the Acanthaceae. Thus he says (1895, p. 281), "Es ist deshalb nur consequent, wenn auf die Pollenbeschaffenheit die Einteilung der A. gegründet wird, wie dies bereits früher von Radlkofer angedeutet wurde und im folgenden ganz streng durchgeführt werden soll". He used the pollen morphology as the basis of his classification of the family in Engler-Prantl, *Die natürlichen Pflanzenfamilien* (1895). He distinguished the following types: "Glatter runder Pollen, Spalten-, Dauben-, Rippen-, Spangen-, Rahmen-, Knötchen-, Stachel-, Gürtel-, Wabenpollen und andere Pollenformen." As a pioneering work, profusely illustrated, it has only to be praised.

Lindau distinguished four subfamilies, Nelsonioideae, Mendoncioideae, Thunbergioideae and Acanthoideae. Later van Tieghem (1908) merged the first three under Thunbergiaceae and separated them from Acanthaceae. Wettstein (1935) was in agreement with this change in so far as that he accepted a close affinity between the three subfamilies, but instead of regarding them as distinct from the Acanthaceae, he considered them as a subfamily Thunbergioideae thus reducing the three subfamilies of Lindau to tribes. In this way he returned to the stand taken by Nees (1847), whose *Anechmatacantheae* and *Echmatacantheae* correspond exactly to Wettstein's Thunbergioideae and Acanthoideae.

During the last few decades many acanthaceous plants have been the subject of detailed pollen morphological study, especially by Bremekamp. This author has made a thorough revision of the family and suggested a number of changes in the classification.

Bremekamp (1938) did not accept van Tieghem's Thunbergiaceae as separate from the Acanthaceae, as he considered that the Mendoncioideae, Thunbergioideae and Acanthoideae formed a natural group (although isolated and therefore better treated as a separate family). He proposed, instead, the division of the Acanthaceae into three subfamilies, Mendoncioideae, Thunbergioideae and Acanthoideae. He did not think it necessary to subdivide the first two subfamilies, as they consist only of a few, closely interrelated

genera. On the other hand he suggested some changes in the subfamily Acanthoideae and thereby modified the sound basis for the sub-division of this group laid down by Nees (l.c.). He furthermore discarded Lindau's division of the Acanthoideae into Contortae and Imbricatae and reduced the 16 tribes distinguished by the same author to seven and arranged them in the following way:—

- | | |
|-------------------|-----------------|
| 1. Acantheae | 5. Ruellieae |
| 2. Trichanthereae | 6. Odontonemeae |
| 3. Isoglosseae | 7. Justicieae |
| 4. Louteridieae | |

Later Bremekamp (1944), having encountered pollen grains of Louteridieae type in some of the Ruellieae, thought it inadvisable to retain Louteridieae as an independent tribe. With regard to Isoglosseae, he found that the differences between this tribe and the Justicieae were too small to justify an independent position for the former and therefore reduced it to a subtribe of the latter. He regretted his earlier reduction of Lindau's subfamily Nelsonioideae to a mere subtribe of the Acantheae; it was no doubt sufficiently distinct to be regarded as an independent tribe. He furthermore restored Andrographideae and Odontonemeae to their former rank on the basis of general morphology and pollen morphological data whilst leaving the position of the tribe Rhombochlamydeae undecided. He also considered the genera *Whitfieldia* Hook., *Stylarthropus* Baill., *Lepidagathis* Willd., and *Herpetacanthus* Nees distinct enough to be regarded as representing separate tribes and thus recognized a total of ten tribes, viz. Nelsonieae, Acantheae, Trichanthereae, Whitfieldieae, Ruellieae, Lepidagathideae, Andrographideae, Herpetacanthae, Odontonemeae and Justicieae.

In the Ruellieae, he now included six of the tribes of Lindau, viz. Louteridieae, Hygrophileae, Petalidieae, Strobilantheae, Ruellieae (with the exception of *Whitfieldia* and *Stylarthropus*) and Barlerieae (with the exception of *Lepidagathis* and its nearest allies).

Lindau's Haselhoffieae, formerly included in the Ruellieae, was excluded and instead Bremekamp suggested a place in the vicinity of the Nelsonieae or in the genera brought together in the Acantheae and thus recognized three subtribes in the Acantheae (Haselhoffiinae, Aphelandrinae and Acanthinae).

He further divided the enlarged Ruellieae into the following six subtribes: Ruelliinae, Barleriinae (*Lepidagathis* and its nearest allies excluded), Hygrophilinae, Blechinae, Petalidiinae and Strobilanthiniae.

The classification adopted in the delimitation of the Justicieae (1944) was later modified (1948) and a more comprehensive group formed (incorporating Lindau's Asystasiaeae, Graptophylleae, Pseudoranthemeae, Odontonemeae and Isoglosseae). On the basis of pollen morphology he retained the tribe Odontonemeae and for the remaining genera he used the name Justicieae. He also proposed the substitution of Isoglossinae by Rhytiglossinae, as Oersted's genus *Isoglossa* was based on the type species of *Rhytiglossa* Nees.

Bremekamp (1953) has discussed the taxonomic position of the Nelsonioideae in detail. "At the moment the best solution seems to be to give the Nelsonioideae a place in the vicinity of the Rhinanthaeae as a tribe Nelsonieae, ..." (l.c., p. 545). Lindau's Mendoncioideae and Thunbergioideae he made into separate families, Mendonciaceae and Thunbergiaceae.

In 1955 (b) Bremekamp further elaborated and defined the Nelsonieae and also described in greater detail the different genera included under it. In 1955 (d) he proposed the division of Lindau's Acanthoideae into two subfamilies, Acanthoideae "sensu Brem." and Ruellioideae. In 1960 he further proposed a new tribe, the Borneacanthae, consisting of the single genus *Borneacanthus* Brem.

The present work is entirely based on pollen morphology. The deflections of the "palynological compass needle" have been recorded and made use of either to substantiate the claims of previous authors or to indicate that some of these claims may not be well founded.

A total of 260 species from 103 genera have been investigated. Detailed diagnoses of 130 species from 98 genera have been provided based on a modern terminology. Thus terms like "Dauben-, Gürtel-, Knötchen-, Rahmen-, Rippen-, Spalten- und Wabenpollen" have been replaced by generally applicable descriptive terms.

Diagnoses of 14 species from 12 genera in the Pedaliaceae have also been given (pp. 65-68). The terminology used is described on pp. 18-23. On the basis of pollen morphology, sundry taxonomical changes have been suggested (pp. 92-99).

The present investigation is a result of an interest, revived and strengthened by the visit of Prof. Gunnar Erdtman to the Osmania University, Hyderabad, India, in 1956. It has been a great privilege to work under his inspiring guidance at the Palynological Laboratory, Solna. His parental care, his encouragement of frank discussion and the interest he has taken in my work has given me an overall impetus. I take this opportunity to express my deep-felt gratitude to him.

Further I am greatly indebted to Prof. C. E. B. Bremekamp, Utrecht, for valuable advice on problems of taxonomic importance and for kindly checking a number of determinations. Finally, I wish to express my sincere thanks to my friends at the Palynological Laboratory who have helped me at all stages of my work, particularly Radwan J. Praglowski.

Materials

The present investigation is based on slides from the "sporotheke" at the Palynological Laboratory of the Swedish Natural Science Research Council, Solna, and a special slide collection made from material received from different sources. At the outset my thanks are due to Prof. Erdtman for helping me to build up this special excellent collection of acanthaceous pollen slides. From his academic visits to various countries, he has sent me both fresh and herbarium material for study, e.g. from Rio de Janeiro, Tucuman and Lima. I am also greatly indebted to my teacher Dr. M. R. Suxena and my colleague Mr. M. R. Saxena, Hyderabad, India, for fresh and herbarium material sent to me from time to time.

I thank Prof. E. Hultén, Director of the Botanical Department of the Riksmuseum, for permitting me to pick herbarium material; Dr. G. Taylor, Director, Royal Botanic Gardens, Kew, for sending 12 pollen-bearing specimens of various acanthaceous genera; Prof. A. Aubréville, Directeur du Laboratoire de Phanérogamie, Muséum National d'Histoire Naturelle, Paris, for sending the rare material of *Pounguia purpurata*; Prof. C. Baehni of the Institut de Botanique Systématique de l'Université, Conservatoire et Jardin Botanique, Genève, for sending the equally very rare material of *Rhombochlamys elata* and *R. rosulata*; Dr. K. N. Kaul, Director, National Botanic Gardens, Lucknow, for fresh material of *Asystasia coromandeliana*.

Preparation of pollen slides

Dry polliniferous herbarium material is crushed on a finely meshed brass screen spread out on a funnel, standing in a test-tube. To the powder collected in the test-tube acetolysis mixture (acetic anhydride 9 parts, concentrated sulphuric acid 1 part) is added drop by drop and stirred thoroughly with a glass rod. The mixture is then heated cautiously to the boiling point in a water bath, stirred at intervals and allowed to stand for a few minutes. After centrifuging at a normal speed, the mixture is decanted and a little water added to the sediment and shaken thoroughly. Foam, if present, is removed by adding a few drops of acetone or alcohol. The mixture is then filtered twice through a finely meshed brass net and centrifuged. After decanting, half of the sediment is taken for chlorination and the other half is made to stand in a few drops of glycerine (50%).

Chlorination is effected by adding about 5 cc. of glacial acetic acid, one or two drops of concentrated sodium chlorate solution and a few drops of concentrated hydrochloric acid and stirred thoroughly with a glass rod. Chlorine appears immediately and bleaching takes place. After centrifuging and decanting, the sediment is washed thoroughly with distilled water in order to eliminate all traces of chlorine. After centrifuging and decanting, a few drops of glycerine (50%) are added. Chlorinated and non-chlorinated grains are then mixed and centrifuged. After decanting, the centrifuge tube is allowed to stand upside down for a while on filter paper.

Slides are made by taking a minute piece of glycerine jelly (made according to Kisser's method) on a clean platinum needle, touching the surface of the pollen-bearing sediment with the jelly cube and then transferring the latter to a clean slide. After gently heating the jelly and spreading it out with the platinum needle, a circular cover-glass is placed on the slide and finally sealed off with solid paraffin (melting point 68–72°C) under the cover-glass.

Whenever possible, herbarium material has been cleaned prior to acetolysis by picking the anthers only. The material of *Haselhoffia nematosiphon*, *Pounguia purpurata*, *Rhombochlamys elata* and *R. rosulata* was so scanty (a single bud only) that the usual procedure had to be modified. Instead, the material was crushed directly in the test-tube with a glass rod, filtration was avoided and the few grains thus obtained were all chlorinated.

Fresh material, fixed either in glacial acetic acid or osmium tetroxide, has been transferred directly from the vials to a finely meshed brass net, resting on a funnel, and crushed. It was then washed down into a test-tube with 70% alcohol and shaken thoroughly. After centrifuging and decanting, acetolysis mixture was added and the above procedure followed. As a rule, all slides have been prepared out of a mixture of acetolyzed non-chlorinated and acetolyzed chlorinated grains, the latter being particularly useful in the study of sporoderm stratification as seen in the optical section. For a more detailed description of the acetolysis method, see Erdtman (1960 b).

Sectioning

Clean polliniferous material, either fresh or acetolyzed, is washed thoroughly in a centrifuge tube with distilled water and gradually dehydrated with alcohol. The material thus treated is allowed to stay overnight in absolute alcohol. The alcohol is then decanted and some methacrylate (methyl methacrylate one part, butyl methacrylate seven parts) is added. Before adding, the methacrylate is washed thoroughly with 2% NaOH solution to remove the stabilizer which retards polymerization. The methacrylate is added three times at an interval of eight to twelve hours and shaken thoroughly quite often to prevent pollen grains from sedimenting. Finally the methacrylate with the proper amount of pollen grains is poured into gelatine capsules.

Hardening of the plastic in the capsules by polymerization is achieved by exposing the capsules, fastened to a tape, to the light produced by a 120 watt UV lamp. During polymerization care is taken to avoid air bubbles from forming in the plastic by keeping the capsules cool by means of a fan (air bubbles can also be formed due to over-concentration of pollen grains or insufficient washing of the pollen material by methacrylate). After about 40-50 hours the plastic is sufficiently hard for cutting.

The gelatine capsules are removed by soaking in water and the plastic units are ready for cutting. A plastic unit is fixed in a holder, in a way so as to expose the pollen bearing part, which is trimmed into a pyramid, the apex of which bears the pollen grains for cutting. The shaping of the pyramid is a very important factor in the process of cutting and involves a certain amount of

skill and experience. To ensure the proper thickness of the sections, the size and number of the pollen grains (even a single grain) have to be taken into consideration and the pyramid carved accordingly (cf. Praglowski, pp. 135–147, in Erdtman 1957).

American "Eversharp" blades are used for cutting. After cleaning the blade with ether, it is mounted in a special holder. The sharpening of the blade by grinding is done on a sheet of plane glass. A suitable amount of grinding powder (type B.5125, Linde Air Products Company) and teepol (one part teepol and four parts distilled water) are thoroughly mixed into a thin paste. Grinding is done with great care and is carried on for 10–15 minutes. After thoroughly washing the knife in running water and absolute alcohol, it is examined under a microscope to ascertain the sharpness of the edge. Before mounting the knife for sectioning, it is allowed to stay for a few minutes in ether to remove the fine particles of the grinding powder which may still be present.

The knife is mounted in a slightly curved position in a special trough. The trough holding the knife is now fixed in the microtome (Spencer Microtome Model 821). After screwing the object-holder tightly into the mobile part of the microtome, a final adjustment of the pyramid in relation to the knife is made. The screw controlling the thickness of the sections is adjusted in accordance with the desired thickness. Final adjusting for sectioning is followed through a binocular microscope ($\times 20$).

The pyramid is brought to the level of the knife by pressure of hand. Great care is taken not to damage the pyramid. The trough holding the knife is filled with distilled water to the brim. The motor is then started. Normally, the sections assemble in the trough, grouping themselves in different ways on the surface of the water. After 10 or more sections have been collected, the motor is stopped and the sections fished up by means of a thin wire, one end of which has been shaped into a small loop. The sections thus fished up are transferred to a drop of distilled water on a clean slide. A piece of filter paper, dipped in chloroform, is held over the sections allowing them to stretch out and lie flat on the slide. The slide with the sections is put away in a dust-free place. After the evaporation of the water, the sections will cling to the surface of the slide which is now transferred to a dish containing acetone. It usually takes 10–12 hours for the plastic surrounding the sections to dissolve. The sections are observed under low magni-

fication ($\times 60$). Good section-bearing areas are marked with a diamond and at the same time dust and debris, if any, carefully removed with a pin. The slide is then carefully rinsed with alcohol and slow running water and transferred to the staining cuvette, filled with basic fuchsin solution. After staining, which usually takes 8–12 hours, the slide is rinsed with water and allowed to dry and is then ready for mounting. Mounting is done by placing minute pieces of glycerine jelly on the sections. A coverslip is then placed on top of each jelly cube and the jelly slowly melted and finally sealed with paraffin wax. When the paraffin has cooled and hardened, the slide is cleaned with a knife and benzol. It has been observed that acetolyzed material takes a better stain than fresh material fixed in glacial acetic acid or osmium tetroxide.

Microscopical investigations have been carried out with optics of Leitz, Wetzlar (apochromat $90\times$, n.A.=1.32; eye-piece $8\times$ periplane). Measurements were made with oil immersion and eye-piece micrometer $6\times$ (1 mark = $1.04\ \mu$).

The illustrations have been drawn to the scale ($\times 1600$) with the aid of a camera lucida, fitted to a monocular microscope (Leitz model A, apochromat $90\times$, n.A.=1.32).

The photographs were taken on panchromatic plates with Leitz Aristophot Ortholux microscope using oil immersion optics ($90\times$, n.A.=1.40, eye-piece $6\times$ periplane), through a medium of glycerine jelly (index of refraction 1.474). Only the following were photographed in water (index of refraction 1.33): *Mendoncia aspera* (Pl. 20, Figs. 4–7) and *Meyenia hawtayneana* (Pl. 21).

The order of photographs shown in the plates is, as a rule, unless otherwise stated, a sequence from the highest focus down to the lowest. "Photopalynograms" have been constructed, wherever possible, by piecing together the pictures at different foci in sequence, so as to give the appearance of a whole grain. The arrangement follows a clockwise pattern usually starting from left side and is numbered accordingly.

As a rule, the figures are the average of 10 measurements of acetolysed grains. "About" is added if they are based on less than 10 measurements.

The order of the genera listed in the Index of plants investigated (pp. 12–17) and of the genera in the Diagnoses of pollen grains (pp. 23–68) are in accordance with Lindau's classification of the Acanthaceae (Lindau 1895 and 1897).

Index of plants investigated

Species marked with an asterisk (*) have been provided with a detailed diagnosis on the page mentioned against their names.

I. Nelsonioideae

1. *Staurogyne concinnula* (Hance) O. Ktze
2. *S. diantheroides* Lindau* (p. 23)
3. *S. mandioccana* (Nees) O. Ktze
4. *Elytraria imbricata* (Vahl) Pers.
5. *E. tridentata* Vahl* (p. 23)
6. *Nelsonia canescens* (Lam.) Spreng.* (p. 23)

II. Mendoncioideae

7. *Mendoncia aspera* (R. et P.) Nees* (p. 24)
8. *M. breviflora* Standl.
9. *M. coccinea* Vell.
10. *M. costaricana* Oerst.
11. *M. lindavii* Britton
12. *M. schomburgkiana* Nees
13. *Monachochlamys flagellaris* Baker* (p. 24)
14. *Gilletiella congolana* De Wild. & Durand* (p. 24)

III. Thunbergioideae

15. *Pounguia purpurata* R. Ben.* (p. 25)
16. *Meyenia hawtayneana* Wall.* (p. 25)
17. *Thunbergia alata* Boj. ex Sims (4 specimens)

18. *T. atriplicifolia* E. Mey.
19. *T. coccinea* Wall.
20. *T. erecta* (Benth.) T. And.
21. *T. fragrans* Roxb., 2 specimens* (p. 26)
22. *T. friesii* Lindau
23. *T. gibsoni* S. Moore
24. *T. grandiflora* Roxb. (3 specimens)
25. *T. laurifolia* Lindl.
26. *T. mysorensis* T. And.
27. *T. sericea* Burkill
28. *T. venosa* C.B.Cl.
29. *T. vogeliana* Benth.
30. *Pseudocalyx africanus* S. Moore* (p. 26)
31. *P. saccatus* Radlk.* (p. 27)

IV. Acanthoideae

Trichanthereae

32. *Sanchezia arborea* Leonard
33. *S. filamentosa* Lindau
34. *S. klugii* Leonard* (p. 27)
35. *S. loranthifolia* Lindau
36. *S. parvibracteata* Sprague & Hutch.
37. *S. peruviana* (DC.) Rusby
38. *S. stenantha* Leonard
39. *Steirosanchezia scandens* Lindau
40. *Bravaisia floribunda* DC.* (p. 28)
41. *B. tubiflora* Hemsl.
42. *Trichanthera gigantea* Nees

Louteridieae

43. *Louteridium donnell-smithii*
Wats.* (p. 28)

Hygrophileae

44. *Mellera lobulata* S. Moore*
(p. 28)
45. *Brillantaisia emini* Lindau*
(p. 29)
46. *B. lamium* Benth.
47. *B. madagascariensis* T. And.
ex Lindau* (p. 29)
48. *Asteracantha longifolia*
Nees* (p. 29)
49. *Hygrophila angustifolia* R.
Br.
50. *H. bayatensis* Urb.* (p. 30)
51. *H. costata* Sinning
52. *H. pringlei* Greenm.
53. *H. spinosa* T. And.

Petalidieae

54. *Blechum brownei* Juss.*
(p. 30)
55. *B. laxiflorum* Juss.
56. *B. laxiflorum* Juss.
57. *Phayloopsis dorsiflora* (Retz.)
Santapau* (p. 31)
58. *P. longifolia* T. Thomas*
(p. 31)
59. *P. oppositifolia* Wendl.*
(p. 31)
60. *Petalidium barlerioides*
Nees* (p. 31)

Strobilantheae

61. *Calophanes amoenus* Nees
62. *C. ciliatus* Nees* (p. 32)
63. *C. hygrophylloides* Nees
64. *C. maranhonis* Nees

65. *C. persoonii* Nees* (p. 32)
66. *C. repens* Nees
67. *Dyschoriste cubensis* Urb.
68. *D. humilis* (Gris.) Lindau
69. *D. oaxacensis* Kobusky
70. *Acanthopale* sp.* (p. 33)
71. *Mimulopsis glandulosa*
(Lindau) Bullock* (p. 33)
72. *Strobilanthes adnatus*
C.B.Cl.
73. *S. alatus* Nees
74. *Sympagis brunoniana* (Nees)
Brem.* (p. 33)
75. *Stenosiphonium russelianum*
Nees* (p. 34)
76. *Aechmanthera gossypina*
(Nees) Nees* (p. 34)

Haselhoffieae

77. *Haselhoffia nematosiphon*
Chev.* (p. 34)

Ruellieae

78. *Forsythiopsis baroni* Bak.*
(p. 35)
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T. And.* (p. 35)
80. *Eranthemum nervosum*
(Vahl) R.Br.* (p. 35)
81. *E. wattii* Stapf
82. *Ruellia acutangula* Nees
83. *R. affinis* Lindau
84. *R. amoena* Nees* (p. 35)
85. *R. angustiflora* Nees*
(p. 36)
86. *R. bahiensis* Nees
87. *R. baurii* C.B.Cl.* (p. 36)
88. *R. brachysiphon* (Nees)
Lindau* (p. 36)
89. *R. capitata* Rizz.

90. *R. formosa* Andr.
 91. *R. graecizans* Backer
 92. *R. hankeana* (Nees) Leonard* (p. 37)
 93. *R. harveyana* Stapf
 94. *R. hirsuta* Nees
 95. *R. longifolia* Rich.* (p. 37)
 96. *R. neesiana* (Mart.) Lindau
 97. *R. nitens* Nees
 98. *R. nudiflora* Urb.
 99. *R. pacifica* Svens.* (p. 37)
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 101. *R. portellae* Hook. f.
 102. *R. prostrata* T. And.
 103. *R. quadrifaria* Lindau
 104. *R. rubicaulis* Cav.
 104 b. *R. speciosa* Mart. ex Nees
 105. *R. tessmannii* Mildbr.* (p. 38)
- Barlerieae*
 106. *Barleria courtallica* Nees* (p. 38)
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 107. *B. lupulina* Lindl.
 108. *B. noctiflora* L. fil.
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 142. *G. coccinea* T. And. ex Griseb.
 143. *G. longiflora* Lindl.
 144. *G. tetragona* Lindau* (p. 43)
 145. *Aphelandra acanthifolia* Hook.

- 146. *A. acutifolia* Nees
- 147. *A. lineariloba* Leonard
- 148. *A. lutea* Nees
- 149. *A. lyrata* Nees* (p. 43)
- 150. *A. montisscalaris* Lindau
- 151. *A. pulcherrima* (Jacq.)
H.B.K.

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Main morphological concepts (cf. also Erdtman & al. 1961)

AMBITUS: equatorial limb, outline of pollen grain viewed with one of the poles exactly uppermost. In isopolar, not constricted grains the maximum ambitus is the same as the equator. In isopolar, equatorially constricted grains the maximum ambitus does not coincide with the equatorial.

Zonotreme (q.v.) pollen grains with more or less angular (or lobate) ambitus are either gonio-, pleuro-, or ptychotreme. In the first case the centres of the apertures are situated at the angles of the ambitus (sides of ambitus slightly convex, straight or concave). In the second case the aperture centres are situated at the midpoints of the sides (sides of ambitus more or less straight). In the third case they are situated in deep grooves (ambitus lobate). In peritreme grains the aperture centres are more or less uniformly distributed along a more or less circular ambitus.

ANOMOTREME: provided with irregular apertures.

APOCOLPIUM: area at a pole, delimited towards the equator by the polar limits of the mesocolpia (q.v.).

APOPORIUM: area at a pole, delimited towards the equator by the polar limits of the mesoporia (q.v.).

BACULA: more or less radial, rod-like elements, e.g. endosexinous rods supporting any ectosexinous elements.

BILATERAL: with two vertical planes of symmetry; equatorial axes not equilong.

BREVISSIMICOLPATE: with very short colpi. Colporate grains are brevisimicolpate if the colpi are as long as or shorter than the underlying circular or lalongate os.

BROCHI: the meshes of a reticulum. A brochus consists of a lumen and the adjoining half of the muri which separate that particular lumen from other lumina.

COLPI: elongate apertures (ratio between longest and shortest axis > 2).

COLPORATE: provided with oriferous colpi.

CRASSINEXINOUS: nexine at least twice as thick as sexine.

CRASSISEXINOUS: sexine at least twice as thick as nexine.

CRASSITEGILLATE: thickness of tegillum twice as great or greater than length of the supporting bacula or depth of the space between tegillum and nexine.

DUPLIBACULATE: with muri provided with two rows of bacula.

ECTONEXINE: the outer, more or less thick, not very refractive part of the nexine.

ECTOSEXINE: the upper (outer, distal) part of the sexine in tegilliferous pollen grains or spores. To the ectosexine belong, e.g. tegilla and suprattegillar processes.

ENDONEXINE: the inner, more or less thin, more refractive part of the nexine.

ENDOSEXINE: the basal (lower, inner, proximal, infrategillar) part of the sexine in tegilliferous pollen grains or spores (what remains if the upper part of the sexine, the ectosexine—q.v.—is removed).

EURYPALYNOUS: said of plant families, etc. characterized by a more or less great array of pollen types (more or less different inter se with regard to apertures, exine stratification, etc.).

EXINE: the main, outer, usually resistant layer of a sporoderm.

GEMMAE: processes deviating from verrucae (q.v.) by having the basal diameter shorter than the longest, non-basal tangential diameter.

GONIOTREME: see *Ambitus*.

GRANULA: granules, often very small and more or less rounded, exinous elements.

HETEROBROCHATE: with brochi of more or less distinctly different size and shape.

HOMOBROCHATE: with brochi of more or less the same size and shape.

INFRATEGILLAR: see *Endosexine* (cf. also Pl. 43, Figs. 7, 9–14).

INSULAE: small, sexinous, usually circular or polygonal areas separated by grooves. Cf. Pl. 43, Figs. 21–24.

INTINE: the innermost, usually not very resistant layer of the sporoderm.

LALONGATE: transversely elongated.

LEPTOMA: thin exine area, functioning as an aperture, but not distinctly delimited as typical apertures.

LOLONGATE: longitudinally elongated.

LUMINA: spaces between the muri of a reticulum.

MESOCOLPIUM: an area delimited by two adjacent colpi and by transverse lines drawn through the apices of the colpi. "Mesocolpium" in a broader sense, see Pl. 42, Fig. 1.

MESOPORIUM: an area delimited by two adjacent pori, in zonoporate pollen grains only, and by their transverse common tangents.

MURI: ridges separating the lumina of an ordinary reticulum.

NEXINE: the inner, usually "non-sculptured" part of the exine.

NOMOTREME: provided with regular apertures (see also Erdtman and Straka 1961).

OBLATE: distinctly flattened. Term used exclusively in descriptions of radiosymmetric, isopolar grains where the ratio between polar axis and equatorial diameter is 0.75–0.50 (6:8–4:8).

OBLATE SPHEROIDAL: this term is used exclusively in descriptions of radiosymmetric, isopolar grains where the ratio between polar axis and equatorial diameter is 1.00–0.88 (8:8–7:8).

Os: the inner or central part of a composite aperture.

PANTOTREME: with apertures uniformly spread over the spore surface.

PARASYNCOLPATE: colpate pollen grains are parasyncolpate if the colpi (or their extensions) are bifurcate and their branches meet more or less close to the poles, leaving intact apocolpia of regular shape.

"PERIPHERAL AREA": see "Trema area".

PERITREME: see Ambitus.

PEROBLATE: very flattened. This term is used exclusively in describing radiosymmetric, isopolar grains where the ratio between polar axis and equatorial diameter is < 0.50 ($< 4:8$).

PERPROLATE: this term denotes exclusively the shape of radiosymmetric, isopolar grains where the ratio between polar axis and equatorial diameter is > 2 ($> 8:4$).

PILA: sculptural elements consisting of more or less swollen apex (caput) and a rod-like neck (baculum).

PLEUROTREME: see *Ambitus*.

POLE: polar grains have two poles, one (the proximal) directed towards the centre of the tetrad, the other (the distal) facing the opposite direction.

POLYBROCHATE: with a large number of brochi (> 45 per ambitus in more or less homobrochate grains).

PORE: more or less circular aperture. The ratio between the longest and the shortest diameter of a pore is 2 or varies from 2 to 1.

PROLATE: this term denotes exclusively the shape of radiosymmetric, isopolar grains where the ratio between polar axis and equatorial diameter is 2–1.33 (8:6–8:7).

PROLATE SPHEROIDAL: this term denotes exclusively the shape of radiosymmetric, isopolar grains where the ratio between polar axis and equatorial diameter is 1.14–1.00 (8:7–8:8).

PSILATE: outer surface of exine smooth.

PTYCHOTREME: see *Ambitus*.

PUNCTITEGILLATE: pollen grains with tegillum or tegilla with minute perforations (puncta) are said to be punctitegillate.

RETICULUM: sexinous pattern consisting of brochi (q.v.). Cf. also Pl. 43, Figs. 1–5.

RETIPIULATE: with a reticuloid pattern with pila instead of muri.

SEXINE: the outer, usually “sculptured” part of the exine.

SIMPLIBACULATE: with muri provided with a single row of bacula.

SPHEROIDAL: in spheroidal grains the ratio between polar axis and equatorial diameter is 0.88–1.14 (7:8–8:7).

SPINES: usually pointed processes (length exceeding $3\ \mu$).

SPINULES: small, pointed processes, not exceeding $3\ \mu$ in length.

SPIROTREME: provided with spiral aperture(s).

SUBOBLATE: term used exclusively in describing radiosymmetric, isopolar grains where the ratio between polar axis and equatorial diameter is 0.75–0.80 (6:8–7:8).

SUBPROLATE: term used exclusively in describing radiosymmetric, isopolar grains where the ratio between polar axis and equatorial diameter is 1.4–1.33 (8:7–8:6).

SUBSPHEROIDAL: comprehensive term for suboblate + oblate spheroidal + prolate spheroidal + subprolate.

SUPRARETICULATE: reticulate pattern due to suprattegillar elements.

SUPRATEGILLAR: sculptural elements rising above the general surface of a tegillum. Cf. Pl. 43: 6 (suprareticulate pattern).

SYNCOLPATE: with colpi anastomosing at the poles.

TECTATE: if a tegillum (or tegilla) covers about 80 per cent or more of the total surface of the pollen grain (apertures not included), the grain is tectate.

TEGILLUM: an ectosexinous, more or less homogeneous layer usually distinctly separated from the nexine by a baculate, infrategillar (endosexinous) zone.

TENUINEXINOUS: with thin nexine, thickness of nexine less than half that of sexine.

TENUISEXINOUS: with thin sexine, thickness of sexine less than half that of nexine.

TENUITEGILLATE: with thin tegillum, thickness of tegillum not more than half the length of the supporting sexinous elements.

“TREMA AREA”: in *Beloperone*, *Justicia*, etc. (cf. e.g. Pl. 6, Figs. 6–9) there is often a striking difference between the areas surrounding the apertures and the rest of the sporoderm surface. In order to avoid lengthy descriptions these areas are referred to as trema areas and peripheral areas.

TUBULI: very fine, usually more or less perpendicular channels running through the nexine or sexine or both.

VERRUCAE: rounded wart-like processes (basal diameter longer than any other tangential diameter, and as long as or longer than the height).

ZONOTREME: with apertures in zonal arrangement.

Diagnoses

Acanthaceae

Nelsonioideae

Staurogyne concinnula (Hance) O. Ktze (Formosa; Suzuki 4490): 3-colpate, prolate ($32 \times 22 \mu$).

S. diantheroides Lindau (Brazil; Malme 1815): 3-colpate (pleurotreme), prolate ($20 \times 14.5 \mu$).

Apocolpium diameter about 8μ . Ambitus triangular (corners of mesocolpia slightly rounded). Colpi about $17 \times 1 \mu$, with tapering ends.

Exine about 2μ thick. Sexine about 1.5μ thick, reticulate (ectosexine about 0.5μ thick). Nexine, as it seems, consists of two layers, ecto- and endonexine.

Reticulum homobrochate. Muri straight, about 0.5μ wide, simplibaculate. Lumina polygonal (about 0.5μ).

S. mandioccana (Nees) O. Ktze (Brazil; Dusén 10166): 3-colpate, prolate ($29 \times 24 \mu$).

Elytraria imbricata (Vahl) Pers. (U.S.A.; Goodding 73-53): 3-colpate, prolate ($40 \times 30 \mu$).

E. tridentata Vahl (Ecuador; Fagerlind & Wibom 106): 3-colpate (pleurotreme), prolate ($37 \times 25 \mu$).

Apocolpium diameter about 8μ . Ambitus rounded, triangular. Colpi about $35 \times 1-2 \mu$, membrane densely granular (granules about $1-2 \mu$).

Exine about 4μ thick throughout. Sexine about 3μ thick, reticulate (ectosexine thicker than endosexine, undulating, about 2μ). Nexine, as it seems, consists of two layers, ecto- and endonexine (inner surface of endonexine uneven).

Reticulum homobrochate. Muri winding, about 1μ wide, simplibaculate. Lumina polygonal to circular (diameter about 1μ).

Nelsonia canescens (Lam.) Spreng. (Nigeria; Hepper 1674): 3-colpate (peritreme), prolate ($25 \times 15 \mu$).

Apocolpium diameter about $8\ \mu$. Ambitus triangular (equatorial contour of mesocolpia slightly convex). Colpi about $18 \times 3\ \mu$, with tapering ends; membrane granular.

Exine about $2.5\ \mu$ thick. Sexine about $2\ \mu$ thick, reticulate (ectosexine undulating, about $0.5\ \mu$ thick). Nexine, as it seems, consists of two layers, ecto- and endonexine.

Mendoncioideae

Mendoncia aspera (R. & P.) Nees (Peru; Klug 2769). Pl. 20, Figs. 4–7.—Pollen grains 5-colporate (brevissimicolpate), goniotreme, prolate spheroidal ($51 \times 47\ \mu$).

Apocolpium diameter about $44\ \mu$. Ambitus pentangular (colpi margins slightly protruding; equatorial contour of mesocolpia slightly convex). Colpi about $11 \times 1\ \mu$; membrane sparsely granular. Ora slightly lolongate ($11 \times 9\ \mu$).

Exine $9\ \mu$ thick, crassinexinous, slightly thicker at ora. Sexine $1\ \mu$ thick, punctitegillate (ectosexine as thick as endosexine). Nexine, as it seems, consists of a thick ecto- and a thin endonexine. See also p. 84.

M. breviflora Standl. (Lawrence 761): 6-colporate, prolate spheroidal ($45 \times 40\ \mu$).

M. coccinea Vell. (Brazil; Mexia 5188): 5-colporate, prolate spheroidal ($45 \times 40\ \mu$).

M. costaricana Oerst. (Br. Honduras; Schipp 1051): 5-colporate, prolate spheroidal ($55 \times 50\ \mu$). For nexine see p. 84.

M. lindavii Britton (Peru; Ferreyra 1894): 5-colporate, prolate spheroidal ($55 \times 50\ \mu$).

M. schomburgkiana Nees (Brazil; Ule 5221): 5-colporate, prolate spheroidal ($45 \times 38\ \mu$).

Monachochlamys flagellaris Baker (Madagascar; "515"): 4-colporate (brevissimicolpate), peritreme, prolate spheroidal ($45 \times 42\ \mu$).

Apocolpium diameter about $40\ \mu$. Colpi about $9 \times 1\ \mu$. Ora lolongate ($8 \times 4\ \mu$).

Exine $3\ \mu$ thick. Sexine about $1\ \mu$ thick, tectate. Tegillum less than $0.5\ \mu$, psilate, supported by short, slender bacula. Nexine, as it seems, consists of two layers, ecto- and endonexine.

Gilletiella congolana De Wild. & Durand (Congo; "540", anno 1900). Pl. 12, Fig. 9.—Pollen grains 3-colpate (occasionally 4-colpate), peritreme, prolate spheroidal ($27 \times 25\ \mu$).

Apocolpium diameter about $20\ \mu$. Colpi about $15 \times 1\ \mu$, with tapering ends; membrane faintly granular.

Exine about $2\ \mu$ thick. Sexine about $1\ \mu$ thick, tectate, or possibly consisting of piloid processes (LO). Nexine, as it seems, forms a single, homogeneous layer.

Thunbergioideae

Pounguia purpurata R. Ben. (Gabon; Le Testu 8166). Pl. 22, Figs. 5, 6.—Pollen grains anomotreme, spheroidal or somewhat flattened (e.g. $47 \times 70\ \mu$). Exine usually provided with two circular areas, about $30\ \mu$ wide, each surrounded by a narrow groove (vestigial spiraperturate condition?). In these areas there are often one or several poroid or colpoid openings (apertures?).

Exine about $6\ \mu$ thick. Sexine about $4\ \mu$ thick, tectate. Tegillum appears to be formed by the amalgamation of densely spaced, slender bacula. Nexine, as it seems, consists of two layers, ecto- and endonexine (in places the inner surface of the endonexine is provided with outgrowths, about $8\ \mu$ long).

Meyenia hawtayneana Wall. (Herb. Wight 2173). Pl. 21, Figs. 1-4.—Pollen grains 8-colpate (occasionally 7- or 9-colpate), peritreme, peroblate ($31 \times 65\ \mu$).

Apocolpium diameter about $36\ \mu$. Ambitus polyangular (equatorial contour of mesocolpia concave; concavities about $9\ \mu$ deep). Colpi about $25 \times 1-2\ \mu$, tenuimarginate (margins uneven), their membrane granular.

Exine about $6\ \mu$ thick. Sexine tectate. For a more detailed description see p. 85.

Thunbergia alata Boj. ex Sims (S. Africa; B. La Vega): spiro-treme, spheroidal (diameter about $85\ \mu$).

T. alata Boj. (cult. Hong Kong): spiro-treme, spheroidal (diameter about $70\ \mu$).

T. alat Boj. (Fiji; Smith 5015): spiro-treme, spheroidal (diameter about $65\ \mu$).

T. alata Boj. (cult. Hyderabad): spiro-treme, spheroidal (diameter about $60\ \mu$).

T. atriplicifolia E. Mey. (Natal; Fisher 1385): spiro-treme, spheroidal (diameter about $85\ \mu$).

T. coccinea Wall. (herb. Mus. Bot. Ups.; Junell): spiro-treme, spheroidal (diameter about $70\ \mu$).

T. erecta (Benth.) T. And. (Cuba; Ekman 13622): spirotreme, spheroidal (diameter about $85\ \mu$).

T. fragrans Roxb. (Haiti; Ekman 16347). Pl. 30, Figs. 8–10.—Pollen grains spirotreme, spheroidal (about $100\ \mu$, processes included), their exine made up of a single, spiral band, about $15\ \mu$ wide.

Exine (processes not included) about $3\ \mu$ thick. Sexine $2\ \mu$ thick, tectate. Tegillum thin (less than $0.5\ \mu$), also covering large, blunt processes (about $15 \times 8\ \mu$). The nexinous substructure of these protrudes towards the interior of the grains causing depressions in the intine. For nexine see also p. 87.

T. fragrans Roxb. (West Indies): spirotreme, spheroidal (diameter, including blunt processes, about $85\ \mu$).

T. friesii Lindau (Rhodesia; Fries 319): spirotreme, spheroidal (diameter about $67\ \mu$).

T. gibsoni S. Moore (cult. Orotava; Sventenius): spirotreme, spheroidal (diameter about $80\ \mu$).

T. grandiflora Roxb. (cult. Orotava; Sventenius): spirotreme, spheroidal (diameter about $75\ \mu$).

T. grandiflora Roxb. (Haiti; Ekman 16476): spirotreme, spheroidal (diameter about $93\ \mu$).

T. grandiflora Roxb. (cult. Copenhagen): spirotreme, spheroidal (diameter about $100\ \mu$).

T. laurifolia Lindl. (Schallert 15100): spirotreme, spheroidal (diameter about $68\ \mu$).

T. mysorensis T. And. (cult. Orotava; Sventenius): spirotreme, spheroidal (diameter about $92\ \mu$).

T. sericea Burkill (Nairobi; Burkill): spirotreme, spheroidal (diameter about $70\ \mu$).

T. venosa C.B. Cl. (Natal; Fisher 747): spirotreme, spheroidal (diameter about $105\ \mu$).

T. vogeliana Benth. (Fernando Po; Mann 557): spirotreme, spheroidal (diameter about $98\ \mu$).

Pseudocalyx africanus S. Moore (Rhodesia; Richards 9008). Pl. 23, Figs. 1–4.—Pollen grains usually spirotreme, spheroidal (about $50\ \mu$, exine made up of a single spiral, about $15\ \mu$ wide).

Exine $5\ \mu$ thick, tenuinexinous. Sexine $4\ \mu$ thick, tectate. Tegillum coarse (about $3\ \mu$ thick), undulating, probably formed by the amalgamation of densely spaced, slender bacula. Nexine, as it seems, consists of a single, granular layer.

P. saccatus Radlk. (Madagascar; Decary 940): spirotreme, spheroidal (about $58\ \mu$); exine made up of a single, spiral band, about $20\ \mu$ wide.

Exine about $5\ \mu$ thick, tenuinexinous. Sexine about $4\ \mu$ thick, tectate. Tegillum about $3\ \mu$ thick, probably formed by the amalgamation of the middle parts of piloid bacula. Nexine, as it seems, consists of a single, granular layer.

Acanthoideae

TRICHANTHEREAE

Sanchezia arborea Leonard (Peru; Ferreyra 4391): 2-porate, bilateral ($92 \times 90 \times 80\ \mu$).

S. filamentosa Lindau (Peru; Ferreyra 13147): 2-porate, bilateral ($82 \times 77 \times 65\ \mu$).

S. klugii Leonard (Peru; Klug 4117). Pl. 28, Figs. 1-4.—Pollen grains 2-porate, bilateral ($70 \times 72 \times 60\ \mu$). Pores lalongate, slightly lolongate or circular (diameter about $8\ \mu$); pore membrane densely granular. Two semicircular, sexinous patches around the apertures suggest the appearance of a narrow, short colpus.

Exine about $5\ \mu$ thick. Sexine about $3\ \mu$ thick (ectosexine about twice as thick as endosexine), made up of three groups of bands. Each group consists of eight bands (the bands are about $1\ \mu$ apart; each band is about $5\ \mu$ wide). Out of the three groups, two are lateral, more or less concentric round the apertures. The third circles round the poles. Sexine in each band reticulate. Reticulum homobrochate. Muri straight, about $1.5\ \mu$ wide, simplibaculate. Some bacula hollow (cf. Figs. 2-3). Lumina (maximum diameter about $1.5\ \mu$) arranged in a single row in the centre of each band.

S. loranthifolia Lindau (Peru; Ule 6820): 2-porate, bilateral ($80 \times 75 \times 60\ \mu$).

S. parvibracteata Sprague & Hutch. (cult. N.Y. Bot. Garden): 2-porate, bilateral ($107 \times 105 \times 95\ \mu$).

S. peruviana (DC.) Rusby (Peru; Ferreyra 7805): 2-porate, bilateral ($90 \times 84 \times 79\ \mu$).

S. stenantha Leonard (Peru; Ridouff 10006): 2-porate, bilateral ($105 \times 92 \times 75\ \mu$).

Steirosanchezia scandens Lindau (Peru; Tessmann 3880): 2-porate, bilateral ($92 \times 80 \times 72\ \mu$).

Bravaisia floribunda DC. (Colombia; Smith 1869): 2-porate, bilateral ($65 \times 62 \times 42 \mu$). Pores circular (about 10μ).

Exine 7μ thick. Sexine 4μ thick (ectosexine thicker than endosexine). For nexine see p. 82. Sexine made up of three groups of bands. Each group consists of about three bands (the bands are about 1μ apart; each band is about 5μ wide). Sexine in each band reticulate. Reticulum homobrochate. Muri straight, about 1μ wide, simplibaculate (bacula of various shapes). Lumina irregular (maximum diameter about 1.5μ) arranged in a single row in the centre of each band.

B. tubiflora Hemsl. (Mexico; Gaumer 618): 2-porate, bilateral ($68 \times 65 \times 55 \mu$).

Trichanthera gigantea Nees (Colombia; Sneidern 2653): 2-porate, bilateral ($101 \times 96 \times 83 \mu$).

LOUTERIDIEAE

Louteridium donnell-smithii Wats. (Brit. Honduras; Lundell 2081). Pl. 19, Figs. 1–3.—Pollen grains pantoporate, spheroidal (about 140μ). Pores \pm circular ($4\text{--}5 \mu$), tenuimarginate. Occasionally there is a faint indication of a short, narrow colpus.

Exine (suprattegillar processes not included) about 12μ thick. Sexine $1\text{--}2 \mu$ thick, tectate. Tegillum less than 0.5μ thick (giving the impression of being formed by the amalgamation of small, piloid processes), provided with gemmae and a few verrucae. Gemmae about 10μ high, provided with pointed protrusions at the base. Gemmae and verrucae seem to consist of a material different from that of the outer wall. They are densely arranged in a few grains and sparsely in a few. Nexine, as it seems, consists of two layers, ecto- and endonexine (inner surface of endonexine uneven).

HYGROPHILEAE

Mellera lobulata S. Moore (Tanganyika; Drummond & Hemsley 1429). Pl. 20, Figs. 1–3.—Pollen grains 3-colporate (peritreme), subprolate ($53 \times 40 \mu$).

Apocolpium diameter about 11μ . Ambitus triangular (colpi margins slightly protruding; equatorial contour of mesocolpia convex). Colpi about $11 \times 4 \mu$, with tapering ends; membrane densely granular. Ora lalongate ($6 \times 9 \mu$). Each mesocolpium has three colpoid

streaks ($50 \times 2 \mu$), which divide it into four bands (about 7μ wide). The bands encircling the colpi form a collar-like thickening around them.

Exine 5μ thick. Sexine about 2.5μ thick, reticulate (ectosexine thinner than endosexine, undulating, about 1μ). Nexine, as it seems, consists of two layers, ecto- and endonexine (inner surface of endonexine uneven).

Reticulum homobrochate. Muri straight, about 1μ wide, simpli-baculate. Lumina hexagonal to circular (maximum diameter about 3μ), occasionally provided with one or two bacula.

Brillantaisia emini Lindau (Uganda; Drummond & Hemsley 4584). Pl. 9, Figs. 1-4.—Pollen grains irregularly 4-colporate (peritreme), prolate spheroidal ($57 \times 52 \mu$).

Apocolpium diameter about 5μ . Colpi about $55 \times 1.5 \mu$, with tapering ends; membrane densely granular. Ora more or less circular (about 5μ). Each mesocolpium provided with four colpoid streaks ($55 \times 2 \mu$) without granules.

Exine about 5μ thick. Sexine about 2μ thick, tectate, supracreticulate (muroid ridges very low, straight, about 0.5μ wide; luminoid areas smooth, maximum diameter about 3μ). Endosexine densely baculate. Nexine, as it seems, consists of two layers, ecto- and endonexine (inner surface of endonexine uneven).

B. lamium Benth. (Sierra Leone; Thomas 2096): 4-colporate, prolate spheroidal ($55 \times 50 \mu$).

B. madagascariensis T. And. ex Lindau (Ethiopia; Mooney 6071): 4-colporate (peritreme), prolate spheroidal ($62 \times 60 \mu$).

Apocolpium diameter about 30μ . Colpi about $40 \times 2 \mu$, with tapering ends; membrane densely granular. Ora elongate ($3 \times 5 \mu$). Each mesocolpium provided with three long, colpoid streaks (about $40 \times 2 \mu$).

Exine (supratrigillar processes not included) about 3μ thick. Sexine 1μ thick, tectate. Trigillum about 0.5μ thick, supported by densely spaced, slender bacula and provided with scattered blunt spinules (about 2μ long). Nexine, as it seems, consists of two layers, ecto- and endonexine.

Asteracantha longifolia Nees (India; Venkatesh): 4-colporate (goniotreme), bilateral ($47 \times 52 \times 40 \mu$).

Apocolpium diameter about 10μ . Ambitus quadrangular (colpi margins slightly protruding; equatorial contour of mesocolpia slightly convex). Colpi about $44 \times 4 \mu$, with tapering ends; mem-

brane densely granular. Ora either circular, lalongate or lolongate (diameter about $9\ \mu$). Each mesocolpium provided with four colloid streaks ($44 \times 1-2\ \mu$).

Exine (reticulum included) about $3\ \mu$ thick. Sexine $1\ \mu$ thick, suprareticulate. Muroid lists straight, less than $0.5\ \mu$ wide. Luminoid smooth, hexagonal to ellipsoidal (maximum diameter about $2-3\ \mu$). For nexine see p. 81.

Hygrophila angustifolia R. Br. (Siam; Zimmermann 81): 3(4)-colporate, prolate spheroidal ($35 \times 33\ \mu$).

H. bayatensis Urb. (Cuba; Ekman 16196): 3-colporate (pleuro-treme), prolate ($55 \times 35\ \mu$).

Apocolpium diameter about $17\ \mu$. Ambitus triangular (colpi margins slightly protruding; equatorial contour of mesocolpia slightly convex). Colpi about $18 \times 1.5\ \mu$. Ora circular (about $5\ \mu$). Each mesocolpium provided with three long, narrow, tapering colloid streaks ($50 \times 1-2\ \mu$). A marked thickening around the colpi can be seen.

Exine about $4\ \mu$ thick. Sexine about $2\ \mu$ thick, tectate. Tegillum supported by densely spaced, slender bacula (ectosexine thinner than endosexine). Nexine, as it seems, consists of two layers, ecto- and endonexine (inner surface of endonexine uneven).

H. costata Sinning (Brazil; Ule 778): 3-colporate, subprolate ($40 \times 34\ \mu$).

H. pringlei Greenm. (Mexico; Pringle 8847): 3-colporate, prolate ($62 \times 41\ \mu$).

H. spinosa T. And. (herb. Mus. Bot. Ups.): 3-colporate, prolate spheroidal ($70 \times 66\ \mu$).

PETALIDIEAE

Blechnum brownei Juss. (Mexico; Fisher 46100). Pl. 7, Figs. 1-4. —Pollen grains 3-colporate (syncolpate), spheroidal (about $47\ \mu$). Colpi about $5\ \mu$ wide at equator; membrane densely granular. Ora circular (about $5\ \mu$).

Exine $4\ \mu$ thick. Sexine $2\ \mu$ thick, reticulate (ectosexine as thick as endosexine). Nexine, as it seems, consists of two layers, ecto- and endonexine.

Reticulum homobrochate. Muri straight, about $1\ \mu$ wide, simplibaculate. Lumina smooth, hexagonal to circular (maximum diameter about $2\ \mu$).

B. laxiflorum Juss. (Mexico; Gaumer 358): 3-colporate (syncolpate), subspheroidal ($48 \times 46\ \mu$).

B. laxiflorum Juss. (Cuba; Moldenke 913): 3-colporate (syncolpate), subspheroidal ($50 \times 45 \mu$).

Phaylopsis dorsiflora (Retz.) Santapau (Rhodesia; Hutchinson & Gillet): 3-colporate (pleurotreme), prolate ($41 \times 28 \mu$).

Apocolpium diameter about 18μ . Colpi about $10 \times 3 \mu$, with tapering ends; membrane densely granular. Ora lalongate ($4 \times 5 \mu$). Each mesocolpium provided with two colpoid streaks ($39 \times 2 \mu$).

Exine 4μ thick. Sexine 1μ thick, reticulate (ectosexine slightly thinner than endosexine). Nexine, as it seems, consists of two layers, ecto- and endonexine (inner surface of endonexine uneven).

Reticulum homobrochate. Muri straight, about 1μ wide, simplibaculate. Lumina smooth, hexangular to circular (maximum diameter about 2μ).

P. longifolia T. Thomas (Rhodesia; Fisher 1604). Pl. 40, Fig. 1.—Pollen grains 3-colporate (pleurotreme), prolate ($42 \times 28 \mu$). Colpi about $8 \times 1 \mu$, short and slit-like; margins not well marked; membrane granular. Ora lalongate ($5 \times 3 \mu$). Each mesocolpium provided with four colpoid streaks ($42 \times 1-2 \mu$), which divide the sexine into bands about 5μ wide. Two semicircular, sexinous patches (about 3μ wide) present on either side of the colpus.

Exine 6μ thick. Sexine 3μ thick, reticulate (ectosexine about 2μ thick, smooth). Nexine, as it seems, consists of two layers, ecto- and endonexine (inner surface of endonexine uneven).

Reticulum homobrochate. Muri straight, about 1μ wide, simplibaculate. Lumina smooth, polygonal to circular (maximum diameter about 2μ).

P. oppositifolia Wendl. (Madagascar; Decary 6590): 3-colporate (pleurotreme), subprolate ($44 \times 34 \mu$). Colpi about $10 \times 1 \mu$, short and slit-like; "patches" present. Ora more or less circular (about 5μ). Each mesocolpium provided with four colpoid streaks ($42 \times 1-2 \mu$), which divide the sexine into bands about 5μ wide.

Exine 4.5μ thick at equator, 3μ at poles. Sexine 3μ thick, reticulate (ectosexine about 1μ thick, slightly undulating). Nexine, as it seems, consists of two layers, ecto- and endonexine.

Reticulum homobrochate. Muri more or less winding, about 1μ wide, simplibaculate. Lumina smooth, polygonal to circular (maximum diameter about 2μ).

Petalidium barlerioides Nees (India; Hooker): 3-colporate (pleurotreme), prolate ($70 \times 50 \mu$).

Apocolpium diameter about 18μ . Colpi about $10 \times 1 \mu$ (occasionally 7μ) with tapering ends; membrane densely granular. There

is a sexinous thickening (about $3\ \mu$) around and along the margins of the colpi. Ora lalongate ($5 \times 6\ \mu$). Each mesocolpium provided with four colpoid streaks ($68 \times 2\ \mu$).

Exine $4-7\ \mu$ thick. Sexine about $2\ \mu$ thick, reticulate (ectosexine thinner than endosexine). Nexine, as it seems, consists of two layers, ecto- and endonexine.

Reticulum homobrochate. Muri straight, about $1\ \mu$ wide, simpli-baculate. Lumina smooth, hexangular to circular (maximum diameter about $0.5\ \mu$).

STROBILANTHEAE

Calophanes amoenus Nees (Brazil; Klein 1116): 3-colporate, prolate ($55 \times 40\ \mu$).

C. ciliatus Nees (Peru; Cerrate & Tovar 10656): 3-colporate (pleurotreme), prolate ($59 \times 36\ \mu$).

Apocolpium diameter about $10\ \mu$. Colpi about $20 \times 1\ \mu$, with tapering ends. Ora lalongate ($3 \times 5\ \mu$). Each mesocolpium provided with six colpoid streaks ($59 \times 1\ \mu$).

Exine $3\ \mu$ thick throughout. Sexine $1\ \mu$ thick, tectate. Tegillum less than $0.5\ \mu$ thick, supported by densely spaced, slender bacula. Nexine, as it seems, consists of two layers, ecto- and endonexine (inner surface of endonexine uneven).

C. hygrophylloides Nees (Parana; Dusén 15640): 3-colporate, prolate ($50 \times 36\ \mu$).

C. maranhonis Nees (Paraguay; Anisits 2647): 3-colporate, prolate ($60 \times 42\ \mu$).

C. persoonii Nees (Natal; Demant 9870): 3-colporate (peritreme), subprolate ($47 \times 38\ \mu$).

Apocolpium diameter about $13\ \mu$. Colpi about $15 \times 4\ \mu$, with tapering ends; membrane granular. Ora lalongate ($10 \times 5\ \mu$). Each mesocolpium provided with about 7 colpoid streaks, about $45\ \mu$ long.

Exine $3\ \mu$ thick. Sexine $1.5\ \mu$ thick, reticulate (ectosexine thinner than endosexine, less than $0.5\ \mu$). Nexine, as it seems, consists of two layers, ecto- and endonexine.

C. repens Nees (Peru; Cerrate & Tovar 10620): 3-colporate, prolate ($56 \times 35\ \mu$).

Dyschoriste cubensis Urb. (Cuba; Ekman 13693): 3-colporate, prolate ($47 \times 28\ \mu$).

D. humilis (Gris.) Lindau (Brazil; Drouet 2378): 3-colporate, subprolate ($55 \times 43 \mu$).

D. oaxacensis Kobusky (Honduras; Yunker 5541): 3-colporate, prolate ($53 \times 35 \mu$).

Acanthopale sp. (Ethiopia; Mooney 6235). Pl. 1, Figs. 1-4.—Pollen grains pantoporate (pores 4 or 6-8), spheroidal (about 97μ). Pores more or less circular (about 5μ); membrane granular.

Exine (blunt, spinoid processes included) about 8μ . Sexine (processes not included) about 1μ thick, densely baculate and provided with scattered spinoid processes. A spinoid process is about 5μ high, apex more or less homogeneous, base 1μ thick and made up of rod-like outgrowths. Nexine, as it seems, consists of two layers, ecto- and endonexine (inner surface of endonexine uneven).

Mimulopsis glandulosa (Lindau) Bullock (Rhodesia; Fisher & Schweickhardt 330): 3-colporate (peritreme), prolate ($71 \times 52 \mu$).

Apocolpium diameter about 8μ . Colpi about $12 \times 4 \mu$, with tapering ends; membrane densely granular. Ora lalongate ($6 \times 9 \mu$). Each mesocolpium provided with six colpoid streaks (the ends of the two marginal ones fuse).

Exine about 5μ thick. Sexine about 2.5μ thick, reticulate (ectosexine thinner than endosexine, about 1μ thick).

Reticulum homobrochate. Muri straight, about 1μ wide, simplibaculate. Lumina smooth, hexangular to circular (maximum diameter about 0.5μ).

Strobilanthes adnatus C.B.Cl. (India; Meebold 7365): 3-colporate, prolate ($50 \times 30 \mu$).

S. alatus Nees (Afghanistan; Aitchison 908): 3-colporate, prolate ($95 \times 60 \mu$).

Sympagis brunoniana (Nees) Brem. (India; Hook.f. & Thompson). Pl. 29, Figs. 12-14.—Pollen grains 3-colporate (peritreme), prolate spheroidal ($60 \times 55 \mu$).

Apocolpium diameter about 45μ . Ambitus triangular (equatorial contour of mesocolpia convex). Colpi about $25 \times 3 \mu$, with tapering ends; their margins sharply wavy; membrane densely granular. Ora lalongate ($8 \times 10 \mu$). Each mesocolpium provided with eight rows of spinules fused to form narrow, wavy ridges, the ends of which are joined in pairs at the apocolpium border. The areas enclosed by these ridges are densely beset with very small processes.

Exine (suprattegillar processes not included) about 7μ thick.

Sexine about $4\ \mu$ thick, tectate. Tegillum about $2\ \mu$ thick, supported by densely spaced, slender bacula and provided with regularly spaced, $2\ \mu$ long spinules. Nexine, as it seems, consists of two layers, ecto- and endonexine.

Stenosiphonium russelianum Nees (India; Wight 2187): 3-colporate (peritreme), prolate ($60 \times 34\ \mu$).

Apocolpium diameter about $10\ \mu$. Colpi about $30 \times 1-2\ \mu$, not quite straight, membrane granular. Ora lalongate (about $5 \times 8\ \mu$). Each mesocolpium provided with four, not quite straight, colpoid streaks (about $45 \times 1.5\ \mu$).

Exine $3\ \mu$ thick. Sexine $2\ \mu$ thick, reticulate (ectosexine thinner than endosexine, less than $0.5\ \mu$). Nexine, as it seems, consists of two layers, ecto- and endonexine (inner surface of endonexine uneven).

Reticulum homobrochate. Muri straight, less than $0.5\ \mu$ wide, simplibaculate. Lumina smooth, hexagonal to circular (maximum diameter about $1.5\ \mu$).

Aechmanthera gossypina (Nees) Nees (herb. Falconer 733): 3-colporate (pleurotreme), prolate to perprolate ($80 \times 40\ \mu$).

Apocolpium diameter about $16\ \mu$. Ambitus triangular (equatorial contour of mesocolpia more or less straight). Colpi about $40 \times 1-2\ \mu$, with tapering ends; membrane densely granular. Ora lalongate ($4 \times 7\ \mu$). Five colpoid streaks per mesocolpium.

Exine $4\ \mu$ thick. Sexine $2\ \mu$ thick, reticulate (ectosexine thinner than endosexine, about $0.5\ \mu$). Nexine, as it seems, consists of two layers, ecto- and endonexine (inner surface of endonexine uneven).

Reticulum heterobrochate. Muri less than $0.5\ \mu$ wide, simplibaculate. Lumina smooth, hexagonal to circular (maximum diameter about $1-3\ \mu$).

HASELHOFFIEAE

Haselhoffia nematosiphon Chev. (Liberia; Chevalier s.n.; herb. Kew; isotype). Pl. 40, Fig. 4.—Pollen grains 3-colpate, prolate (about $65 \times 45\ \mu$). Colpi about $38 \times 4\ \mu$, with tapering ends; membrane densely granular (granules about $2-3\ \mu$). Each mesocolpium provided with two long, narrow colpoid streaks (about $47 \times 4\ \mu$).

Exine about $5\ \mu$ thick. Sexine about $3\ \mu$ thick, baculate. Bacula about $0.5\ \mu$ high, densely spaced, supporting a thick, smooth tegillum with a delicate OL-pattern. Nexine, as it seems, consists of two layers, ecto- and endonexine.

RUELLIEAE

Forsythiopsis baroni Bak. (Madagascar; Baron 1737). Pl. 12, Figs. 1-4.—Pollen grains 3-colporate (goniotreme), prolate ($60 \times 40 \mu$).

Apocolpium diameter about 17μ . Colpi about $55 \times 2 \mu$, with tapering ends; membrane granular. Ora lolongate ($4 \times 2 \mu$). Each mesocolpium with two long, colpoid streaks about 11μ from colpi.

Exine 4μ thick. Sexine 3μ thick, reticulate (ectosexine thinner than endosexine). Nexine, as it seems, consists of a thin, homogeneous layer.

Reticulum homobrochate. Muri straight, about 1μ wide, simplibaculate. Lumina smooth, polygonal (maximum diameter about 1μ).

Whitfieldia longifolia T. And. (Nigeria; Kennedy 613). Pl. 30, Figs. 11-13.—Pollen grains pantoporate (pores 5, 6 or more than 6), spheroidal (diameter about 70μ). Pores circular (about 5μ); membrane densely granular (granules about $1-2 \mu$).

Exine (supratégillar processes included) about 8μ thick. Sexine 5μ thick, tectate. Tegillum about 4μ thick, supported by slender bacula and beset with sparsely spaced spinules (about 2μ long, about 1μ broad at base; base circular). Nexine, as it seems, consists of two layers, ecto- and endonexine (inner surface of endonexine uneven).

Eranthemum nervosum (Vahl) R. Br. (cult. N.Y. Bot. Garden): 3-porate, spheroidal (diameter about 105μ). Pores more or less circular.

Exine about 19μ thick. Sexine about 15μ thick, reticulate (ectosexine thinner than endosexine, about 5μ thick). Nexine homogeneous.

Reticulum homobrochate. Muri winding, about 5μ wide, simplibaculate. Bacula provided with a small, apical hollow. Lumina irregular (longest axis $11-21 \mu$), occasionally provided with a few processes.

E. wattii Stapf (cult. N.Y. Bot. Garden): 3-porate, spheroidal (diameter about 100μ).

Ruellia acutangula Nees (Brazil; Dusén 17786): 3-porate, spheroidal (diameter about 65μ).

R. affinis Lindau (Brazil; Malme 852): 3-porate, spheroidal (diameter about 64μ).

R. amoena Nees (Copenhagen; Erdtman). Pl. 41, Fig. 1.—Pollen

grains 3-porate, spheroidal (diameter about $61\ \mu$). Pores more or less circular (about $5\ \mu$).

Exine $5\ \mu$ thick. Sexine $4\ \mu$ thick, reticulate (ectosexine as thick as endosexine). Nexine, as it seems, consists of a thin, homogeneous layer.

Reticulum homobrochate. Muri sharply winding, about $1.5\ \mu$ wide, duplibaculate; bacula with hollows at apex and base. Lumina more or less polygonal (maximum diameter about $7\ \mu$), occasionally provided with a few bacula.

R. angustiflora Nees (Brazil; Lindman 909). Pl. 25, Figs. 5–8.—Pollen grains 3-porate (occasionally there is an indication of a faint colpus at each aperture), spheroidal (about $57\ \mu$). Pores lolongate ($5 \times 3\ \mu$); membrane faintly granular.

Exine $8\ \mu$ thick. Sexine $7\ \mu$ thick, reticulate (ectosexine about $2\ \mu$ thick). Nexine, as it seems, consists of a thin, homogeneous layer.

Reticulum homobrochate. Muri more or less straight, about $2\ \mu$ wide, simplibaculate; bacula branched at apex. Lumina polygonal (maximum diameter about $9\ \mu$), occasionally provided with three or four bacula.

R. bahiensis Nees (Brazil; Dusén 10585): 3-porate, spheroidal (diameter about $55\ \mu$).

R. baurii C.B. Cl. (S. Africa; Fisher 756): 3-porate, spheroidal (diameter about $47\ \mu$). Pores more or less circular (about $5\ \mu$); membrane granular.

Exine $4\ \mu$ thick. Sexine $3\ \mu$ thick, reticulate (ectosexine thinner than endosexine, about $2\ \mu$ thick). Nexine, as it seems, consists of a thin, homogeneous layer.

Muri with very thin crests, sharply winding, about $1\ \mu$ wide, duplibaculate. Lumina more or less polygonal (maximum diameter about $8\ \mu$), provided with densely spaced, small processes.

R. brachysiphon (Nees) Lindau (Brazil; Dusén 10975). Pl. 26, Figs. 1–4.—Pollen grains 3-porate, spheroidal (diameter about $83\ \mu$). Pores lolongate ($6 \times 3\ \mu$); membrane faintly granular.

Exine $12\ \mu$ thick. Sexine about $9\ \mu$ thick, reticulate (ectosexine undulating, about $5\ \mu$). Nexine, as it seems, consists of a thin, homogeneous layer.

Reticulum homobrochate. Muri sharply winding, about $1.5\ \mu$ wide, simplibaculate; bacula branched at apex. Lumina polygonal (maximum diameter about $20\ \mu$), provided with a few processes.

R. capitata Rizz. (Brazil; "3677"): 3-porate, spheroidal (diameter about 85 μ).

R. formosa Andr. (cult. Kew; Erdtman): 3-porate, spheroidal (diameter about 60 μ).

R. graecizans Backer (Brazil; "3348"). Pl. 26, Figs. 5–8.—Pollen grains 3-porate, spheroidal (diameter about 55 μ).

R. hankeana (Nees) Leonard (Peru; Ferreyra 4329; det. Leonard): 3-porate, spheroidal (diameter about 70 μ). Pores circular or slightly lolongate (about 6 μ).

Exine 8 μ thick. Sexine about 7 μ thick, reticulate (ectosexine about 3 μ thick). Nexine, as it seems, consists of a thin, homogeneous layer.

Reticulum polybrochate. Muri winding, about 2 μ wide (their margins crenelated, if seen from above), simplibaculate. Lumina polygonal to circular (maximum diameter about 9 μ), occasionally provided with one or two processes.

R. harveyana Stapf (Brazil; Lundell 6667): 3-porate, spheroidal (diameter about 72 μ).

R. hirsuta Nees (Brazil; "3299"): 3-porate, spheroidal (diameter about 78 μ).

R. longifolia Rich. (Brazil; Dusén 45): 3-porate (there is an indication of a colpus at each aperture), spheroidal (diameter about 51 μ). Pores more or less lalongate.

Exine about 5 μ thick. Sexine about 4 μ thick, reticulate (ectosexine as thick as endosexine or slightly thinner). Nexine, as it seems, consists of a thin, homogeneous layer.

Reticulum homobrochate. Muri sharply winding, about 1.5 μ wide, duplibaculate (occasionally simplibaculate). Lumina polygonal to circular (maximum diameter about 6 μ), provided with densely spaced processes.

R. neesiana (Mart.) Lindau (Brazil; Williams 6776): 3-porate, spheroidal (diameter about 99 μ).

R. nitens Nees (Brazil; "3610"): 3-porate, spheroidal (diameter about 87 μ).

R. nudiflora Urb. (Haiti): 3-porate, spheroidal (diameter about 55 μ).

R. pacifica Svens. (Peru; Ferreyra 7061). Pl. 27, Figs. 1–5.—Pollen grains 3-porate, spheroidal (diameter about 70 μ). Pores more or less circular (about 10 μ); occasionally there is an indication of a faint colpus at each aperture.

Exine about $6\ \mu$ thick. Sexine about $5\ \mu$ thick, reticulate (ectosexine about $2\ \mu$ thick). Nexine, as it seems, consists of a thin, homogeneous layer.

Reticulum homobrochate. Muri faintly winding, about $1.5\ \mu$ wide, simplibaculate. Lumina polygonal to circular (maximum diameter about $10\ \mu$), densely spaced with small processes.

R. patula Jacq. (Nairobi; Wall 55): 2–3-porate or pantoporate (4–7), spheroidal (diameter about $52\ \mu$).

R. portellae Hook. f. (cult. Hort. Berg.; Erdtman): 3-porate, spheroidal (diameter about $69\ \mu$).

R. prostrata T. And. (Mozambique; Faulkner 344): 3-porate, spheroidal (diameter about $55\ \mu$).

R. quadrifaria Lindau (Peru; Ferreyra 7979): 3-porate, spheroidal (diameter about $73\ \mu$).

R. rubicaulis Cav. (cult. N.Y. Bot. Garden): 3-porate, spheroidal (diameter about $89\ \mu$).

R. tessmannii Mildbr. (Peru; Ferreyra 1149). Pl. 41, Fig. 2.—Pollen grains 3-porate, spheroidal (diameter about $89\ \mu$). Pores circular (outline and membrane cannot be easily distinguished due to the reticulum).

Exine $18\ \mu$ thick. Sexine $16\ \mu$ thick, reticulate (ectosexine about $4\ \mu$ thick). Nexine, as it seems, consists of a thin, homogeneous layer. See also p. 86.

Reticulum homobrochate. Muri winding, about $2\ \mu$ wide, simplibaculate. Bacula sometimes branched, often with hollows at apex and base. Maximum diameter of lumina about $25\ \mu$.

BARLERIEAE

Barleria courtallica Nees (India; Meebold 8279). Pl. 39, Fig. 2.—Pollen grains 3-porate, subprolate ($127 \times 107\ \mu$). Pores lolongate ($10 \times 5\ \mu$).

Exine about $21\ \mu$ thick. Sexine about $15\ \mu$ thick, reticulate. Nexine, as it seems, consists of a thick, homogeneous layer.

Reticulum homobrochate. Muri winding, about $2\ \mu$ wide, simplibaculate. Lumina more or less hexangular (maximum diameter about $35\ \mu$).

B. lupulina Lindl. (Haiti; Ekman 276): 3-porate, spheroidal (diameter about $102\ \mu$).

B. noctiflora L. fil. (cult. Kew; Erdtman): 3-porate, spheroidal (diameter about $105\ \mu$).

B. prionitis L. (Tanganyika; Schlieben 2409): 3-porate, spheroidal (diameter about $90\ \mu$).

Barleriola multiflora Urb. (Haiti; Ekman 5459). Pl. 6, Figs. 1-5. —Pollen grains 3-colporate (pleurotreme), prolate ($72 \times 50\ \mu$).

Apocolpium diameter about $12\ \mu$. Colpi about $45 \times 1-2\ \mu$, with pointed ends; membrane granular. Ora circular (about $4\ \mu$).

Exine about $8\ \mu$ thick, tenuinexinous. Sexine about $5.5\ \mu$ thick, reticulate (ectosexine about $2\ \mu$ thick, slightly undulating). Nexine, as it seems, consists of two layers, ecto- and endonexine (inner surface of endonexine uneven).

Reticulum heterobrochate. Muri about $2-3\ \mu$ wide, simplibaculate. Bacula about $3 \times 1\ \mu$, with a small hollow at the apex. Lumina irregular (maximum diameter about 10 and $5\ \mu$), smaller towards apertures and corners. Big lumina densely spaced with processes.

B. solanifolia (L.) Oerst. (Haiti; Ekman 447): 3-colporate, prolate ($41 \times 30\ \mu$).

Crabbea acaulis N.E. Brown (Natal; Tosh 34): 2-porate, spheroidal (about $57\ \mu$). Pores more or less circular (about $6\ \mu$); membrane densely granular. Pore margins densely spaced with small processes.

Exine about $5\ \mu$ thick. Sexine about $3\ \mu$ thick, reticulate (ectosexine thicker than endosexine, about $2\ \mu$ thick). Nexine, as it seems, consists of two layers, ecto- and endonexine (inner surface of endonexine uneven).

Reticulum fragmentimurate. Muri winding, about $2\ \mu$ wide, simplibaculate. Lumina irregular (maximum diameter about $14\ \mu$), provided with processes of varying size.

C. hirsuta Harv. (Natal; Fisher 550): 2-porate, spheroidal (about $60\ \mu$). Pores more or less circular (about $6\ \mu$); membrane granular; margins densely spaced with small processes.

Exine about $6\ \mu$ thick. Sexine about $3\ \mu$ thick, reticulate, in places retipilate (ectosexine about $2\ \mu$ thick). Nexine, as it seems, consists of two layers, ecto- and endonexine.

Reticulum homobrochate. Muri winding, about $1.5\ \mu$ wide, simplibaculate. Lumina more or less polygonal (maximum diameter about $11\ \mu$), densely spaced with bacula of varying size.

Lepidagathis alopecuroides R. Br. (Guatemala; von Türckheim 573): 3-colporate (pleurotreme), prolate ($32 \times 22\ \mu$).

Apocolpium diameter about $9\ \mu$. Colpi about $23 \times 2\ \mu$. Ora lolongate ($5 \times 3\ \mu$).

Exine $4\ \mu$ thick. Sexine about $2\ \mu$ thick, reticulate (ectosexine slightly undulating, about $0.5\ \mu$ thick). Nexine, as it seems, consists of two layers, ecto- and endonexine.

Reticulum heterobrochate. Muri winding, about $1\ \mu$ wide, simplibaculate. Lumina irregular (maximum diameter about $2\text{--}5\ \mu$). Lumina smaller along the colpi margins; larger lumina occasionally provided with a few processes.

Lophostachys falcata Nees (Brazil; Macêdo 7975). Pl. 18, Figs. 1–4.—Pollen grains 3-colporate (pleurotreme), prolate ($65 \times 36\ \mu$).

Apocolpium diameter about $14\ \mu$. Colpi $50 \times 5\ \mu$, with tapering ends; membrane smooth. Ora circular (about $5\ \mu$).

Exine $5\ \mu$ thick. Sexine about $2.5\ \mu$ thick, reticulate (ectosexine less than $0.5\ \mu$ thick). Nexine, as it seems, consists of two layers, ecto- and endonexine (inner surface of endonexine uneven).

Reticulum homobrochate. Muri straight, about $1\ \mu$ wide, simplibaculate. Lumina often hexangular (maximum diameter about $8\ \mu$), densely spaced with processes.

L. floribunda Pohl (Brazil; Lindman 3307): 3-colporate, prolate ($72 \times 42\ \mu$).

L. mufersa Rusby (Paraguay; Balansa 2446): 3-colporate, prolate ($45 \times 31\ \mu$).

ACANTHEAE

Blepharis asperrima Nees (India; Hook. f. & Thomas): 3-colpate (pleurotreme), prolate ($42 \times 21\ \mu$).

Apocolpium diameter about $9\ \mu$. Colpi about $35 \times 2\text{--}3\ \mu$, with tapering ends; margins uneven; membrane faintly granular.

Exine about $4\ \mu$ thick. Sexine about $2\ \mu$ thick, tectate. Tegillum less than $0.5\ \mu$ thick, supported by slender bacula. Nexine, as it seems, consists of three layers.

B. boerhaviaefolia Pers. (India, Hyderabad; Saxena). Pl. 7, Figs. 5–8.—Pollen grains 3-colpate (peritreme), prolate ($60 \times 30\ \mu$).

Apocolpium diameter about $20\ \mu$. Colpi about $54 \times 1\text{--}2\ \mu$, with tapering ends; margins uneven; membrane faintly granular.

Exine about $4\ \mu$ thick at poles, $5\ \mu$ at centre of mesocolpia. Sexine about $2\ \mu$ thick at poles, $3\ \mu$ at centre of mesocolpia, reticulate (ectosexine slightly undulating, about $1.5\ \mu$ thick). For nexine see p. 82.

Reticulum homobrochate. Muri straight, about $0.5\ \mu$ wide, simpli-

baculate. Lumina smooth, polygonal (maximum diameter about $3\ \mu$).

B. edulis Pers. (Pappi 1379): 3-colpate, prolate ($40 \times 21\ \mu$).

B. molluginifolia Pers. (India, Hyderabad; Saxena): 3-colpate, prolate ($35 \times 20\ \mu$). For nexine see p. 82.

Acanthus arboreus Forsk. (Ethiopia; Gillet 14483). Pl. 2, Figs. 1-4.—Pollen grains 3-colpate (pleurotreme), perprolate ($46 \times 23\ \mu$).

Apocolpium diameter about $3\ \mu$. Colpi about $40 \times 2\ \mu$, with tapering ends; margins uneven; membrane faintly granular.

Exine about $3\ \mu$ thick. Sexine about $1\ \mu$ thick, reticulate (ectosexine slightly undulating, less than $0.5\ \mu$). Nexine, as it seems, consists of three layers.

Reticulum homobrochate. Muri straight, less than $0.5\ \mu$ wide, simplibaculate. Lumina polygonal (maximum diameter about $1\ \mu$), with a single process in the middle.

A. dioscoridis L. (Iraq; Regel 30): 3-colpate, perprolate ($57 \times 28\ \mu$).

A. hirsutus Boiss. (Africa; Steppberg): 3-colpate, prolate ($58 \times 30\ \mu$).

A. hungaricus Boiss. (Yugoslavia; Krebs s.n.): 3-colpate, prolate ($53 \times 23\ \mu$).

A. ilicifolius L. (Java; Mellerborg). Pl. 3, Figs. 1-4.—Pollen grains 3-colpate (pleurotreme), prolate ($54 \times 30\ \mu$).

Apocolpium diameter about $14\ \mu$. Colpi about $52 \times 2\ \mu$, with tapering ends; membrane granular.

Exine about $4\ \mu$ thick. Sexine about $2\ \mu$ thick, retipilate—reticulate (ectosexine slightly undulating, about $0.5\ \mu$). Nexine, as it seems, consists of two layers, ecto- and endonexine.

Reticulum homobrochate. Muri winding, about $1\ \mu$ wide, simplibaculate. Lumina polygonal to circular (maximum diameter about $1-2\ \mu$), densely studded with small processes.

A. leucostachyus Wall. (India; Griffith 6147): 3-colpate, perprolate ($63 \times 23\ \mu$).

A. longifolius Poir. (Brazil; Pejovic): 3-colpate (pleurotreme), prolate ($57 \times 32\ \mu$).

Apocolpium diameter about $13\ \mu$. Colpi about $44 \times 2\ \mu$, with tapering ends; margins uneven; membrane faintly granular.

Exine about $3\ \mu$ thick. Sexine about $1\ \mu$ thick, reticulate (ectosexine less than $0.5\ \mu$ thick). Nexine, as it seems, consists of three layers.

Reticulum homobrochate. Muri straight, less than $0.5\ \mu$ wide, simplibaculate. Lumina polygonal (maximum diameter about $1\ \mu$), provided with a single process in the middle.

A. syriacus Boiss. (Syria; Aaronsohn & Täckholm 416): 3-colpate, perprolate ($56 \times 26\ \mu$).

Crossandra greenstockii S. Moore (Natal; Tosh 22): 3-colpate (pleurotreme), perprolate ($48 \times 20\ \mu$).

Apocolpium diameter about $5\ \mu$. Colpi about $37 \times 2\ \mu$, with tapering ends; membrane granular.

Exine about $4\ \mu$ thick. Sexine about $2\ \mu$ thick, reticulate (ectosexine less than $0.5\ \mu$ thick). Nexine, as it seems, consists of a homogeneous layer.

Reticulum homobrochate. Muri straight, about $1\ \mu$ wide, simplibaculate. Lumina polygonal to circular (maximum diameter about $1\ \mu$).

C. nilotica Oliver (cult. Hort. Berg.): 3-colpate, prolate ($75 \times 40\ \mu$).

C. undulaefolia Salisb. (cult. Copenhagen): 3-colpate, perprolate ($80 \times 30\ \mu$). For nexine see p. 82.

C. warneckii S. Moore (Tanganyika; Drummond & Hemsley 5355): 3-colpate, perprolate ($54 \times 23\ \mu$).

Sclerochiton boivini (Baill.) C.B. Cl. (Amami; Verdcourt). Pl. 29, Figs. 1–7.—Pollen grains 3-colpate (pleurotreme), subprolate ($43 \times 34\ \mu$), with 3-radiate depressions at poles (Figs. 5–7).

Apocolpium diameter about $7\ \mu$. Colpi about $42 \times 5\ \mu$, with tapering ends; membrane densely granular.

Exine $2\ \mu$ thick at poles, $3\ \mu$ at centre of mesocolpia. Sexine $1\ \mu$ thick at poles, $1\ \mu$ at centre of mesocolpia, punctitegillate. Tegillum less than $0.5\ \mu$ thick. Nexine, as it seems, consists of two layers, ecto- and endonexine (inner surface of endonexine very uneven).

S. harveyanus Nees (Rhodesia; Fisher 1242): 3-colpate, subprolate ($35 \times 27\ \mu$). Polar depressions. Sexine punctitegillate.

APHELANDREAE

Stenandrium barbatum Torr. & Gray (Texas; McVaugh 8147): 3-colpate, goniotreme (pleurotreme?), prolate ($48 \times 30\ \mu$). Colpi about $45 \times 4\ \mu$, with rounded ends.

Exine $2\ \mu$ thick. Sexine $1\ \mu$ thick, tectate. Tegillum about $0.5\ \mu$ thick, supported by densely spaced, slender bacula.

S. droseroides Nees (Cuba; Ekman 12827): 3-colpate, prolate ($35 \times 20 \mu$), finely reticulate. Apocolpia very small.

S. pohlii Nees (Brazil; Malme 2501): pantoporate (6 or 7), spheroidal (diameter about 40μ). Apertures indistinct. Exine verrucose.

S. trinerve Nees (Uruguay; Lorentz 915). Pl. 29, Figs. 8–11.—Pollen grains anomotreme, with irregular, weak, leptomatoid zones, spheroidal (about 32μ).

Exine (including suprategillar processes) about 5μ thick. Sexine about 2μ thick, tectate. Tegillum less than 0.5μ thick, provided with scattered verrucae (about 3μ wide), surrounded by smaller processes. Nexine thin, homogeneous.

Geissomeria cincinnata Nees (Brazil; Malme 3438): 3-colpate, perprolate ($69 \times 24 \mu$).

G. coccinea T. And. ex Griseb. (Jamaica; Harris 12861): 3-colpate, prolate ($65 \times 39 \mu$).

G. longiflora Lindl. (Brazil; Dusén 708): 3-colpate, perprolate ($66 \times 21 \mu$).

G. tetragona Lindau (Brazil; Malme 7994). Pl. 12, Figs. 5–8.—Pollen grains 3-colpate (pleurotreme), perprolate ($77 \times 30 \mu$).

Apocolpium diameter about 10μ . Colpi about $75 \times 3\text{--}5 \mu$, with tapering ends.

Exine about 3μ thick. Sexine about 1.5μ thick, reticulate. Nexine, as it seems, consists of a single, homogeneous layer.

Reticulum homobrochate. Muri winding, about 1μ wide, simplibaculate. Lumina polygonal to circular (maximum diameter about $2\text{--}3 \mu$).

Aphelandra acanthifolia Hook. (Ecuador; Rimbach 630): 3-colpate, perprolate ($66 \times 26 \mu$).

A. acutifolia Nees (Peru; Tessmann 5517): 3(4)-colpate, perprolate ($80 \times 45 \mu$).

A. lineariloba Leonard (Mexico; Mexia 8952): 3-colpate, prolate ($48 \times 27 \mu$).

A. lutea Nees (Brazil; Ule 4588): 3-colpate, perprolate ($77 \times 31 \mu$).

A. lyrata Nees (Peru; Ferreyra 12955). Pl. 39, Fig. 1.—Pollen grains 3-colpate (pleurotreme), perprolate ($64 \times 23 \mu$).

Apocolpium diameter about 11μ . Colpi about $60 \times 3 \mu$ (occasionally 6μ wide), with tapering ends.

Exine 2.5μ thick. Sexine about 1μ thick, reticulate (ectosexine

less than $0.5\ \mu$ thick). Nexine, as it seems, consists of two layers, ecto- and endonexine.

Reticulum homobrochate. Muri more or less straight, less than $1\ \mu$ wide, simplibaculate. Lumina hexangular to circular (less than $1\ \mu$), occasionally provided with one or two processes.

A. montisscalaris Lindau (Peru; Ule 6558): 3-colpate, perprolate ($75 \times 28\ \mu$).

A. pulcherrima (Jacq.) H.B.K. (Peru; Ferreyra 4494): 3-colpate, perprolate ($69 \times 25\ \mu$).

RHOMBOCHLAMYDEAE

Rhombochlamys elata Lindau (Colombia; Lehmann 2891). Pl. 25, Figs. 1-4.—Pollen grains 3-colpate (peritreme), prolate ($51 \times 30\ \mu$).

Apocolpium diameter about $6\ \mu$. Ambitus triangular (equatorial contour of mesocolpia slightly convex). Colpi about $45 \times 10\ \mu$, with tapering ends; membrane incrassate, with same sexine pattern as the mesocolpia, but with a narrow, marginal, densely and finely granular part.

Exine $2\ \mu$ thick at poles, $3\ \mu$ at centre of mesocolpia. Sexine $1\ \mu$ thick at poles and $2\ \mu$ at centre of mesocolpia, reticulate (ectosexine thinner than endosexine, slightly undulating). Nexine, as it seems, consists of two layers, ecto- and endonexine (inner surface of endonexine uneven).

Reticulum homobrochate. Muri straight, about $0.5\ \mu$ wide, simplibaculate. Mesocolpial lumina usually hexangular (diameter about $1\ \mu$), smaller towards the apertures.

R. rosulata Lindau (Colombia; Lehmann 2197): 3-colpate, prolate ($50 \times 32\ \mu$).

ANDROGRAPHIDEAE

Phlogacanthus curviflorus Nees (Burma; Meebold 16645). Pl. 40, Fig. 3.—Pollen grains 3-colporate (peritreme), prolate ($48 \times 27\ \mu$).

Apocolpium diameter about $20\ \mu$. Ambitus rounded triangular. Colpi about $37 \times 4\ \mu$, with tapering ends; membrane densely granular in the os region (granules about $1-2\ \mu$ thick); margins of colpi thickened, densely spaced with small processes. Ora lalongate ($3 \times 5\ \mu$).

Exine $3\ \mu$ thick. Sexine about $2\ \mu$ thick, reticulate (ectosexine less than $0.5\ \mu$). For nexine see p. 85.

Reticulum homobrochate. Muri about $0.5\ \mu$ wide. Lumina hexagonal to circular (maximum diameter about $2\ \mu$), provided with densely spaced processes.

P. pubinervius T. And. (China; Forrest 26203): 3-colporate (pleurotreme), prolate ($46 \times 30\ \mu$).

Apocolpium diameter about $7\ \mu$. Colpi about $43 \times 3\ \mu$, with tapering ends; membrane densely granular in the os region (granules about $2-3\ \mu$ thick); margins of colpi uneven, provided with short, blunt processes. Ora lalongate (about $4 \times 6\ \mu$).

Exine $3\ \mu$ thick. Sexine about $2\ \mu$ thick, reticulate (ectosexine less than $0.5\ \mu$). Nexine, as it seems, consists of two layers, ecto- and endonexine.

Reticulum homobrochate. Muri winding, solid, about $1\ \mu$ wide. Lumina polygonal (maximum diameter about $7\ \mu$), provided with densely spaced, very small processes.

Andrographis echiioides Nees (India, Hyderabad; Saxena). Pl. 4, Figs. 1-5.—Pollen grains 3-colporate (pleurotreme), prolate ($52 \times 36\ \mu$).

Apocolpium diameter about $12\ \mu$. Colpi about $47 \times 10\ \mu$, with tapering ends; margins thickened (about $3\ \mu$), except at the equator, where the colpi are slightly constricted; membrane densely granular. Ora lalongate (about $7 \times 10\ \mu$).

Exine $3\ \mu$ thick. Sexine $1.5\ \mu$ thick, reticulate (ectosexine less than $0.5\ \mu$). Nexine, as it seems, consists of two layers, ecto- and endonexine (inner surface of endonexine uneven).

Reticulum homobrochate. Muri straight, about $1\ \mu$ wide, simplibaculate. Lumina hexangular to circular (maximum diameter about $3\ \mu$), provided with densely spaced processes.

A. paniculata Nees (Jamaica; Webster 4997): 3-colporate, prolate (about $37 \times 22\ \mu$).

Cystacanthus turgidus Nichols. (Indo-China; Squires 846). Pl. 11, Figs. 1-4.—Pollen grains 3-colporate (pleurotreme), prolate ($43 \times 30\ \mu$).

Apocolpium diameter about $20\ \mu$. Colpi about $34 \times 3\ \mu$, with tapering ends, margins thickened, except at the tapering ends, densely beset with small processes; membrane densely granular. Ora lalongate (about $4 \times 8\ \mu$).

Exine $3\ \mu$ thick. Sexine about $2\ \mu$ thick, reticulate (ectosexine less than $0.5\ \mu$). Nexine, as it seems, consists of two layers, ecto- and endonexine (inner surface of endonexine uneven).

Reticulum homobrochate. Muri straight, about $1\ \mu$ wide, simplibaculate. Lumina hexagonal to circular (maximum diameter about $2\ \mu$), provided with one or two processes.

ASYSTASIEAE

Thomandersia laurifolia (Benth.) Baill. (Nigeria; Onochie 33225). Pl. 30, Figs. 4–7.—Pollen grains 5-colpate (occasionally 6-colpate), peritreme, oblate ($44 \times 58\ \mu$).

Apocolpium diameter about $30\ \mu$. Colpi about $39\ \mu$.

Exine about $4\ \mu$ thick. Sexine about $3\ \mu$ thick, reticulate (ectosexine about $2\ \mu$ thick, formed by the amalgamation of capita, supported by densely spaced, slender bacula). Nexinous thickenings parallel to colpi.

Reticulum homobrochate. Muri slightly winding, about $1\ \mu$ wide, simplibaculate. Lumina more or less circular (maximum diameter about $1\ \mu$).

Chalarothyrsus amplexicaulis Lindau (Mexico; Hinton & al. 7624): 3-colporate (goniotreme), prolate ($62 \times 40\ \mu$).

Apocolpium diameter about $15\ \mu$. Colpi about $36 \times 3\ \mu$, with tapering ends; membrane granular. Ora circular (about $5\ \mu$). Mesocolpia with two colpoid streaks ($60\ \mu$), about $6\ \mu$ sideways from colpi.

Exine about $3\ \mu$ thick. Sexine about $1\ \mu$ thick, suprareticulate. Tegillum less than $0.5\ \mu$ thick, supported by densely spaced bacula. Muroid ridges winding, less than $0.5\ \mu$ wide, simplibaculate. Luminoid areas circular (maximum diameter less than $3.5\ \mu$). Nexine, as it seems, consists of two layers, ecto- and endonexine (inner surface of endonexine uneven).

Spathacanthus hoffmanni Lindau (Costa Rica; Skutch 3325): 3-colporate (goniotreme), subprolate ($71 \times 60\ \mu$).

Apocolpium diameter about $30\ \mu$. Ambitus triangular (equatorial contour of mesocolpia straight). Colpi about $40 \times 7\ \mu$, with tapering ends; membrane densely granular (granules about $2\text{--}3\ \mu$). Oralongate (about $12 \times 15\ \mu$). Each mesocolpium provided with two long, narrow, colpoid streaks (about $71 \times 2\text{--}3\ \mu$), which occasionally anastomose.

Exine about $5\ \mu$ thick. Sexine about $3\ \mu$ thick, tectate. Tegillum about $1\ \mu$ thick, supported by densely spaced, slender bacula. For nexine see p. 86.

Styasasia sp. (Tanganyika; Drummond & Hemsley 1923). Pl. 30,

Figs. 1-3.—Pollen grains 5-porate, spheroidal (about $50\ \mu$). Pores circular (about $5\ \mu$); membrane granular.

Exine (supratégillar processes not included) about $5\ \mu$ thick. Sexine about $2\ \mu$ thick, tectate. Tegillum less than $0.5\ \mu$, supported by densely spaced, slender, short bacula, and provided with densely spaced spinules (about 1.5 – $2\ \mu$ long). Nexine, as it seems, consists of two layers, ecto- and endonexine.

Asystasia bella Benth. & Hook. f. (cult. Orotava; Sventenius): 3-porate, prolate spheroidal ($59 \times 56\ \mu$).

A. coromandeliana Nees (cult. Bot. Gdns Lucknow). Pl. 5, Figs. 1-5.—Pollen grains 3-porate (pleurotreme), prolate ($87 \times 48\ \mu$).

Pores circular (about $4\ \mu$); membrane granular.

Exine $5\ \mu$ thick at poles and pores, $11\ \mu$ at mesoporia centres. Sexine $2\ \mu$ thick at poles, up to $6\ \mu$ at equator, reticulate (ectosexine as thick as endosexine or thinner). For nexine see p. 81.

Reticulum homobrochate. Muri straight, about $1.5\ \mu$ wide, simplibaculate—simplibaculariate. According to the LO-patterns some of the bacula seem to have a hollow base (Pl. 5, Fig. 3). Lumina more or less circular (maximum diameter about $2\ \mu$).

"Trema area" about $87 \times 18\ \mu$, provided with three colpoid streaks (87×1 – $5\ \mu$), gradually tapering towards the pores. Two are on either side of the pores and the third is in line with the same meridian as the pores and widens into a more or less circular area (about $10\ \mu$) around the latter. This area is provided with small processes, densely spaced along the contour of the pore.

A. gangetica (L.) T. And. (Amani; Verdcourt): 3-porate, prolate ($68 \times 42\ \mu$).

A. nemorum Nees (cult. Bogor; Fagerlind): 3-porate, prolate ($65 \times 41\ \mu$).

A. schimperi T. And. (Nairobi; Meuse 10302): 3-porate, prolate ($59 \times 40\ \mu$).

Chamaeranthemum beyrichii Nees (Brazil; Widgren 687): 3-colporate (peritreme), subprolate ($52 \times 45\ \mu$).

Apocolpium diameter about $5\ \mu$. Colpi about $50 \times 8\ \mu$, with tapering ends; membrane densely granular (granules about $4\ \mu$). Ora lolongate (about $8 \times 5\ \mu$). Each mesocolpium provided with five long, narrow, colpoid streaks (about 50×1 – $2\ \mu$).

Exine about $3\ \mu$ thick. Sexine about $2\ \mu$ thick, suprareticulate. Tegillum about $0.5\ \mu$ thick. Nexine, as it seems, consists of two layers, ecto- and endonexine.

Reticulation "homobrochate". Muroid ridges, about $0.5\ \mu$ wide, simplibaculate. Luminoid areas polygonal to circular (maximum diameter about $2-3\ \mu$).

Hulemacanthus whitei S. Moore (cult. Bogor; Fagerlind). Pl. 14, Figs. 1-4.—Polien grains 3-colporate (pleurotreme), subprolate ($77 \times 60\ \mu$).

Apocolpium diameter about $26\ \mu$. Colpi about $58 \times 10\ \mu$, with tapering ends; membrane densely granular (granules about $1-2\ \mu$). Ora circular (about $6\ \mu$).

Exine $2.5-6\ \mu$ thick. Sexine $1.5\ \mu$ thick, reticulate (ectosexine less than $0.5\ \mu$).

Reticulum heterobrochate. Muri winding, about $1-1.5\ \mu$ wide, simpli- or duplibaculate. Lumina hexagonal to circular (maximum diameter about $5\ \mu$), densely spaced with small processes.

GRAPTOPHYLLEAE

Ruspolia decurrens (Hochst. ex Nees) Milne-Redhead (Rhodesia; Chase 638): 3-colporate (peritreme), prolate spheroidal ($59 \times 52\ \mu$).

Apocolpium diameter about $11\ \mu$. Colpi about $57 \times 6\ \mu$, with tapering ends; membrane slightly granular. Ora lolongate (about $10 \times 6\ \mu$). Each mesocolpium provided with two long, narrow, colpoid streaks ($1-2\ \mu$ wide), their ends joined towards the apocolpium.

Exine about $3\ \mu$ thick. Sexine about $2\ \mu$ thick, reticulate (ectosexine undulating, about $0.5\ \mu$ thick). Nexine, as it seems, consists of two layers, ecto- and endonexine.

Reticulum homobrochate. Muri straight, about $1\ \mu$ wide, simplibaculate. Lumina polygonal to circular (maximum diameter about $2\ \mu$).

Graptophyllum hortense Nees (herb. Mus. Bot. Ups.): 3-colporate (peritreme), prolate spheroidal ($70 \times 62\ \mu$).

Apocolpium diameter about $15\ \mu$. Colpi about $65 \times 3\ \mu$, with tapering ends; membrane granular. Ora more or less circular (about $7\ \mu$), contour faintly marked. Each mesocolpium with two colpoid streaks (about $59 \times 2\ \mu$), about $10\ \mu$ sideways from colpi.

Exine $6\ \mu$ thick. Sexine $4\ \mu$ thick, reticulate (ectosexine less than $0.5\ \mu$). Nexine, as it seems, consists of two layers, ecto- and endonexine.

Reticulum homobrochate. Muri straight, about $1\ \mu$ wide, simplibaculate. Lumina irregular (maximum diameter about $3\ \mu$).

G. insularum (A. Gray) A. C. Smith (Fiji; Smith 5574): 3-porate, subprolate ($55 \times 46 \mu$). Pores lolongate (about $10 \times 7 \mu$), tenuimarginate, each situated in the centre of a faint, longitudinal, colpoid streak ($40 \times 7 \mu$); membrane densely granular (a few granules about $2-3 \mu$). Each "mesocolpium" provided with two longitudinal, colpoid streaks (about $1-2 \mu$ wide), their ends joined towards the "apocolpia".

Exine about 5μ thick. Sexine 2.5μ thick, reticulate (ectosexine thinner than endosexine, less than 0.5μ). Nexine, as it seems, consists of two layers, ecto- and endonexine.

Reticulum homobrochate. Muri straight, about 1μ wide, simplibaculate. Lumina polygonal to circular (about 1μ).

G. pictum (L.) Griff. (Haiti; Brass 27310): 3-porate, subprolate ($72 \times 60 \mu$). Pores lolongate (about $12 \times 8 \mu$), tenuimarginate, each situated in the centre of a faint, longitudinal, colpoid streak ($50 \times 8 \mu$); membrane densely granular. Each "mesocolpium" provided with two longitudinal, colpoid streaks, their ends joined towards the "apocolpia".

Exine about 4μ thick. Sexine about 2μ thick, reticulate (ectosexine less than 0.5μ). For nexine see p. 83.

Reticulum homobrochate. Muri straight, about 0.5μ wide, simplibaculate. Lumina polygonal to circular (maximum diameter about 1μ).

Pachystachys lutea Nees (Peru; Ferreyra 1675): 3-colporate, perprolate ($65 \times 32 \mu$).

P. riedeliana Nees (Ecuador; Haught 3484): 3-colporate (pleurotreme), prolate ($79 \times 54 \mu$).

Apocolpium diameter about 20μ . Colpi about $60 \times 10 \mu$, with tapering ends; membrane densely granular (granules about 2μ). Ora slightly lalongate (about $8 \times 10 \mu$). Each mesocolpium with two colpoid streaks (about $65 \times 2-3 \mu$), about 8μ sideways from colpi.

Exine about 5μ thick. Sexine about 2μ thick, suprareticulate (ectosexine thinner than endosexine, undulating, less than 0.5μ). Nexine, as it seems, consists of two layers, ecto- and endonexine.

Reticulation "heterobrochate". Muroid ridges winding, about 1μ wide. Luminoid areas irregular (maximum diameter about 8μ and 2μ), provided with 5-9 marginal puncta.

Carlwrightia californica Budge. (California; Gentry 4331). Pl. 40, Fig. 2.—Pollen grains 3-colporate (pleurotreme), prolate ($38 \times 25 \mu$).

Apocolpium diameter about $17\ \mu$. Colpi about $36 \times 4\ \mu$, with tapering ends; membrane densely granular (granules about $1\ \mu$). Ora more or less circular (about $5\ \mu$). Each mesocolpium provided with two long, narrow, colpoid streaks (about $36 \times 1-2\ \mu$).

Exine about $4\ \mu$ thick. Sexine about $2\ \mu$ thick, reticulate (ectosexine undulating, about $0.5\ \mu$). Nexine, as it seems, consists of two layers, ecto- and endonexine.

Reticulum homobrochate. Muri straight, about $0.5\ \mu$ wide, simplibaculate. Lumina polygonal to circular (maximum diameter about $1-2\ \mu$).

Anisacanthus abditus Bodge. (Mexico; Gentry 1178): 3-colporate, prolate ($55 \times 34\ \mu$).

Apocolpium diameter about $12\ \mu$. Colpi about $53 \times 6\ \mu$, with tapering ends; membrane sparsely granular. Ora lalongate (about $4 \times 7\ \mu$). Each mesocolpium provided with two long, narrow, colpoid streaks (about $53 \times 1.5\ \mu$).

Exine about $4\ \mu$ thick. Sexine about $2\ \mu$ thick, reticulate (ectosexine less than $0.5\ \mu$ thick). Nexine, as it seems, consists of two layers, ecto- and endonexine (inner surface of endonexine uneven).

Reticulum homobrochate. Muri straight, less than $0.5\ \mu$ wide, simplibaculate. Lumina hexangular (about $2-3\ \mu$), provided with many processes.

A. malmei Lindau (Paraguay; Lindman 2123): 3-colporate, subprolate ($43 \times 37\ \mu$).

A. thurberi (Torr.) Gray (Mexico; Gentry 1309): 3-colporate, prolate ($77 \times 53\ \mu$).

Thamnojusticia sp. (Tanganyika; Drummond & Hemsley 2094): 2-porate, bilateral ($43 \times 32 \times 28\ \mu$). Pores lalongate (about $6 \times 8\ \mu$), each situated in the centre of a colpoid streak (see below). Pore membrane densely granular.

Exine about $4\ \mu$ thick at poles, $5\ \mu$ at equator, provided with six longitudinal, colpoid streaks. The poriferous streaks have tapering ends and measure about $43 \times 8\ \mu$. The others are found about $5\ \mu$ sideways from each apertural colpoid streak. Sexine about $2\ \mu$ thick, punctitegillate. Tegillum undulating, provided with funnel-like depressions. Under each depression is a stout baculum. In a narrow belt in the surface of the funnels a great number of puncta can be seen which traverse the tegillum obliquely. Nexine, as it seems, consists of two layers, ecto- and endonexine (inner surface of endonexine uneven).

Chlamydocardia buettneri Lindau (Nigeria; Talbot 1374). Pl. 10, Figs. 1–3.—Pollen grains 6-colporate, spheroidal (diameter about $60\ \mu$). Colpi about $25 \times 1\ \mu$, with tapering ends; membrane granular. Ora circular (about $3\text{--}4\ \mu$).

Exine (supratragillar processes not included) about $6\ \mu$ thick at poles, $4\ \mu$ at centre of mesocolpia. Sexine $3\ \mu$ thick at poles, $1\ \mu$ at centre of mesocolpia, tectate. Tegillum less than $0.5\ \mu$ thick, supported by densely spaced, slender bacula, and beset with densely spaced, blunt processes (about $2\ \mu$ long). Bacula gradually shorter towards apertures. Nexine, as it seems, consists of two layers, ecto- and endonexine (inner surface of endonexine uneven).

PSEUDERANTHEMEAE

Pseuderanthemum cordatum (Nees) Radlk. (Paraguay; Hassler 8024): 3-colporate (peritreme), prolate spheroidal ($45 \times 42\ \mu$).

Apocolpium diameter about $25\ \mu$. Colpi about $30 \times 3\ \mu$, with tapering ends; membrane granular. Ora lolongate (about $6 \times 5\ \mu$). Each mesocolpium provided with two long, narrow, colpoid streaks (about $25 \times 1\ \mu$).

Exine about $4\ \mu$ thick. Sexine about $2\ \mu$ thick, reticulate (ectosexine less than $0.5\ \mu$). Nexine, as it seems, consists of two layers, ecto- and endonexine (inner surface of endonexine uneven).

Muri faintly winding, less than $0.5\ \mu$ wide, probably simplibaculate. Lumina irregular (about $1\text{--}2\ \mu$).

P. cuatrecasasii Leonard (Colombia): 3-colporate (peritreme), subprolate ($31 \times 25\ \mu$).

Apocolpium diameter about $14\ \mu$. Colpi about $30 \times 3\ \mu$; membrane densely granular (granules about $1\ \mu$, largest near the os). Ora circular (about $4\ \mu$). Each mesocolpium provided with two long, narrow, colpoid streaks, their ends joined towards the apocolpium.

Exine about $3\ \mu$ thick. Sexine about $1.5\ \mu$ thick, reticulate (ectosexine less than $0.5\ \mu$). Nexine, as it seems, consists of two layers, ecto- and endonexine.

Reticulum homobrochate. Muri straight, less than $0.5\ \mu$ wide, simplibaculate. Lumina polygonal to circular (maximum diameter about $1\ \mu$).

P. malaccense Lindau (Siam; Zimmermann 104). Pl. 22, Figs. 7–11.—Pollen grains 3-colporate (peritreme), prolate spheroidal ($52 \times 48\ \mu$).

Apocolpium diameter about $11\ \mu$. Colpi about $45 \times 4\ \mu$, with tapering ends; membrane densely granular (granules about $1-2\ \mu$). Ora more or less circular (about $5\ \mu$).

Exine about $5\ \mu$ thick. Sexine about $3\ \mu$ thick, reticulate (ectosexine slightly undulating, about $1\ \mu$ thick). Nexine, as it seems, consists of two layers, ecto- and endonexine.

Muri about $2\ \mu$ wide, simplibaculate. Lumina polygonal to circular (maximum diameter about $6\ \mu$), provided with densely spaced, small processes (less than $0.5\ \mu$).

Mackaya bella Harv. (Uruguay; Sein 19684): 3-colporate (peritreme), prolate spheroidal ($50 \times 48\ \mu$).

Apocolpium diameter about $12\ \mu$. Colpi about $40 \times 4\ \mu$, with tapering ends; membrane densely granular. Ora more or less circular (about $5\ \mu$). Each mesocolpium provided with two long, narrow, colpoid streaks (about $40 \times 1\ \mu$), their ends usually joined towards the apocolpium.

Exine about $5\ \mu$ thick. Sexine about $2.5\ \mu$ thick, reticulate (ectosexine undulating, about $1\ \mu$ thick). Nexine, as it seems, consists of two layers, ecto- and endonexine (inner surface of endonexine uneven).

Reticulum homobrochate. Muri slightly winding, about $1\ \mu$ wide, simplibaculate. Lumina polygonal to circular (maximum diameter about $2\ \mu$).

Sapphoa rigidifolia Urb. (Cuba; Ekman 3844): 3-colporate (peritreme), prolate spheroidal ($49 \times 44\ \mu$).

Apocolpium diameter about $10\ \mu$. Colpi about $48 \times 2-3\ \mu$; membrane densely granular (granules about $2\ \mu$). Ora lolongate (about $10 \times 5\ \mu$). Each mesocolpium provided with two long, narrow, colpoid streaks (about $44 \times 1-2\ \mu$).

Exine about $4\ \mu$ thick. Sexine about $2\ \mu$ thick, reticulate (ectosexine undulating, about $1\ \mu$ thick). Nexine, as it seems, consists of two layers, ecto- and endonexine.

Reticulum homobrochate. Muri winding, about $1\ \mu$ wide, simplibaculate. Lumina polygonal to circular (maximum diameter about $1.5\ \mu$).

Codonacanthus pauciflorus Nees (Assam; Kingdon Ward 7817): 4-colporate (peritreme), suboblate (about $38 \times 44\ \mu$). Colpi short, slit-like (about $7 \times 1-2\ \mu$); membrane densely granular. Ora more or less circular (about $5\ \mu$).

Exine about $5\ \mu$ thick. Sexine about $2\ \mu$ thick, suprareticulate

(ectosexine thicker than endosexine, sharply undulating). Nexine, as it seems, consists of two layers, ecto- and endonexine (inner surface of endonexine uneven).

Reticulation "homobrochate". Muroid ridges slightly undulating, less than $0.5\ \mu$ wide. Luminoid areas irregular (less than $0.5\ \mu$).

Ptyssiglottis parviflora Ridley (Malaya; Kloss s.n.): 3-colporate (peritreme), prolate spheroidal ($45 \times 40\ \mu$).

Apocolpium diameter about $18\ \mu$. Colpi about $40 \times 6\ \mu$, with tapering ends; membrane granular (a few granules about $2-3\ \mu$). Ora circular (about $5\ \mu$). Each mesocolpium provided with two colpoid streaks (about $35\ \mu$ long).

Exine about $4\ \mu$ thick. Sexine about $2\ \mu$ thick, reticulate (ectosexine as thick as endosexine, slightly undulating). Nexine, as it seems, consists of two layers, ecto- and endonexine.

Reticulum homobrochate. Muri about $1.5\ \mu$ wide, simplibaculate. Lumina more or less circular (maximum diameter about $1.5\ \mu$).

ODONTONEMEAE

Ballochia amoena Balf. f. (Socotra; Schweinfurth 780): 3-colporate (peritreme), spheroidal to oblate spheroidal (about $47 \times 48\ \mu$).

Apocolpium diameter about $5\ \mu$. Colpi about $45 \times 4\ \mu$, with tapering ends; membrane granular. Ora lolongate (about $10 \times 5\ \mu$). Each mesocolpium provided with two long, narrow, colpoid streaks (about $40 \times 2\ \mu$), about $6\ \mu$ sideways from colpi.

Exine $5\ \mu$ thick, crassimarginate. Sexine $2\ \mu$ thick, reticulate (ectosexine thinner than endosexine, slightly undulating, about $0.5\ \mu$ thick). Nexine, as it seems, consists of two layers, ecto- and endonexine (inner surface of endonexine uneven).

Reticulum homobrochate. Muri winding, about $1\ \mu$ wide, simplibaculate. Lumina polygonal to circular (maximum diameter about $2\ \mu$).

Ruttya ovata Harv. (Natal; Bayer 1492): 3-colporate (peritreme), oblate spheroidal ($46 \times 49\ \mu$).

Apocolpium diameter about $10\ \mu$. Colpi about $41 \times 2-3\ \mu$, with tapering ends; membrane densely granular. Ora lolongate (about $7 \times 5\ \mu$). Each mesocolpium provided with two long, narrow, colpoid streaks (about $41 \times 1-2\ \mu$), about $9\ \mu$ sideways from colpi.

Exine $5\ \mu$ thick. Sexine $2\ \mu$ thick, reticulate (ectosexine smooth, less than $0.5\ \mu$). Nexine, as it seems, consists of two layers, ecto- and endonexine (inner surface of endonexine uneven).

Reticulum homobrochate. Muri straight, less than $1.5\ \mu$ wide, simplibaculate (bacula large). Lumina polygonal to circular (maximum diameter about $1.5\ \mu$).

Monothecium aristatum T. And. (Tanganyika; Drummond & Hemsley 1931): 3-colporate (pleurotreme), subprolate ($25 \times 20\ \mu$).

Apocolpium diameter about $7\ \mu$. Colpi about $20 \times 3\ \mu$, with tapering ends; membrane slightly granular. Ora circular (about $4\ \mu$). Each mesocolpium provided with two long, narrow, colpoid streaks (about $16 \times 1-3\ \mu$).

Exine (suprattegillar processes included) about $3\ \mu$. Sexine about $1.5\ \mu$ thick, tectate, at poles faintly suprareticulate. Tegillum less than $0.5\ \mu$ thick, provided with very small, pointed spinules.

Hypoestes antennifera S. Moore (Stellenbosch 15011; Jordaan mis.). Pl. 15, Figs. 1-5.—Pollen grains 3-colporate (pleurotreme), prolate ($61 \times 38\ \mu$).

Apocolpium diameter about $8\ \mu$. Colpi about $58 \times 1-2\ \mu$, with tapering ends; membrane faintly granular. Ora circular (about $3\ \mu$). Each mesocolpium provided with two long, narrow, colpoid streaks (about $59 \times 1\ \mu$), about $5\ \mu$ sideways from colpi.

Exine $6\ \mu$ thick. Sexine $4\ \mu$ thick, punctitelligillate. Tegillum undulating, $3\ \mu$ thick (seems to be formed by the amalgamation of the upper parts of faintly funnel- or mushroom-shaped processes; cf. Pl. 42, Fig. 2). Nexine, as it seems, consists of two layers, ecto- and endonexine.

H. aristata (Vahl) Roem. & Schult. (Ethiopia; Mooney 5491): 3-colporate, prolate ($58 \times 32\ \mu$).

H. verticillaris (L. fil.) Roem. & Schult. (Tanganyika; Drummond & Hemsley 2913): 3-colporate, prolate ($44 \times 25\ \mu$).

Peristrophe bivalvis (L.) Merr. (China; Steward & Cheo 812): 3-colporate, subprolate ($61 \times 51\ \mu$).

P. natalensis T. And. (Natal; Akett 3): 3-colporate, prolate ($54 \times 35\ \mu$).

Apocolpium diameter about $16\ \mu$. Colpi about $50 \times 4\ \mu$, with tapering ends; membrane slightly granular. Ora circular (about $4\ \mu$). Each mesocolpium provided with two long, narrow, colpoid streaks (about $50 \times 1\ \mu$), about $5\ \mu$ sideways from colpi.

Exine $3\ \mu$ thick at poles, $5\ \mu$ at centre of mesocolpia. Sexine $2\ \mu$ thick at poles, $3\ \mu$ at centre of mesocolpia, punctitelligillate. Tegillum less than $0.5\ \mu$ thick, smooth, supported by stout bacula (diameter up to $2\ \mu$, circumference irregular).

P. speciosa Nees (cult. N.Y. Bot. Garden): 3-colporate, prolate ($75 \times 54 \mu$).

Tetramerium glandulosum Oerst. (Mexico; Pringle 6174): 3-colporate (pleurotreme), prolate ($45 \times 27 \mu$).

Apocolpium diameter about 10μ . Colpi about $40 \times 7 \mu$, with tapering ends; membrane densely granular. Ora lalongate (about $5 \times 7 \mu$). Each mesocolpium provided with two long, narrow, colpoid streaks (about $40 \times 2 \mu$).

Exine 3μ thick. Sexine 1.5μ thick, reticulate (ectosexine less than 0.5μ thick). Nexine, as it seems, consists of two layers, ecto- and endonexine.

Reticulum heterobrochate. Muri straight, less than 0.5μ wide, simplibaculate. Lumina hexagonal to circular (maximum diameter about 1.5μ), each with one or several processes.

Rungia blumeana Val. var. *hirsuta* Val. (Java; Möller): 2-porate, bilateral ($29 \times 20 \times 12 \mu$). Pores lalongate (about $3 \times 5 \mu$); membrane granular.

Exine 2μ thick at poles, 3μ at equator. Sexine 1μ thick at poles, 2μ at equator (in peripheral area), tectate. Equatorial ectosexine thicker than the baculate endosexine.

"Trema area" circular (about 10μ), studded with circular insulae (about $1-2 \mu$), showing a very small, reticulate pattern.

R. grandis T. And. (Congo; Jessérant 861): 2-porate, bilateral ($40 \times 35 \times 25 \mu$). "Peripheral area" reticulate. "Trema areas" insulate.

R. parviflora Nees (India): 2-porate, bilateral (longest axis about 30μ).

Dicliptera assurgens (L.) Juss. (Haiti; Purpus 12076): 3-colporate, perprolate ($61 \times 25 \mu$).

D. chinensis Juss. (China; Dahlström 194): 3-colporate, prolate ($50 \times 30 \mu$).

D. heterostegia Presl (Natal; Comins 201): 3-colporate, prolate ($55 \times 37 \mu$).

D. niederleiniana Lindau (Bolivia; Kuntze s.n.): 3-colporate, prolate ($50 \times 25 \mu$).

D. resupinata Juss. (Bolivia; Kuntze s.n.): 3-colporate, prolate ($50 \times 25 \mu$).

D. scutellata Griseb. (Argentina; Schickendantz 72): 3-colporate (pleurotreme), prolate ($57 \times 32 \mu$).

Apocolpium diameter about 10μ . Ambitus rounded triangular. Colpi about $51 \times 3 \mu$, with tapering ends. Ora lalongate (about

$2 \times 4 \mu$). Each mesocolpium provided with two long, narrow, colpoid streaks (about $51 \times 2 \mu$), about 5μ sideways from colpi.

Exine 2μ thick at poles, 4μ at centre of mesocolpia. Sexine 1μ thick at poles, 3μ at centre of mesocolpia, punctitegillate. Tegillum undulating, less than 0.5μ thick, supported by bacula. Nexine, as it seems, consists of two layers, ecto- and endonexine (inner surface of endonexine uneven).

D. suberecta (E. André) Brem. (cult. Kew): 3-colporate, prolate ($67 \times 42 \mu$).

Juruasia rotundata Lindau (Brazil; Ule 5573): 3-colporate (peritreme), spheroidal (about 44μ).

Apocolpium diameter about 17μ . Colpi about $22 \times 1-4 \mu$, with tapering ends; membrane granular. Ora circular (about 5μ). Each mesocolpium provided with two colpoid streaks (about $22 \times 1 \mu$), about 8μ sideways from colpi.

Exine 4μ thick. Sexine about 2μ thick, reticulate (ectosexine undulating, less than 1.5μ). Nexine, as it seems, consists of two layers, ecto- and endonexine (inner surface of endonexine uneven).

Reticulum homobrochate. Muri winding, about 0.5μ wide, simpli-baculate. Lumina polygonal to circular (maximum diameter about $1-2 \mu$).

Odontonema callistachyum (S. & C.) Kuntze (Mexico; Ekman 8037): 3-colporate (pleurotreme), subprolate ($51 \times 41 \mu$).

Apocolpium diameter about 13μ . Colpi about $50 \times 1 \mu$, with tapering ends; membrane granular. Ora circular (about 6μ). Each mesocolpium with six colpoid streaks (about 46μ long).

Exine 3μ thick. Sexine 1.5μ thick, reticulate (ectosexine smooth, less than 0.5μ). Nexine, as it seems, consists of two layers, ecto- and endonexine (inner surface of endonexine uneven).

Reticulum homobrochate. Muri straight, about 1μ wide, simpli-baculate. Lumina hexangular to circular (maximum diameter about $1-2 \mu$).

Ecbolium oreadam OK. (Brazil; Kuntze s.n.): 2-porate, bilateral ($42 \times 27 \times 23 \mu$). Pores lalongate (about $4 \times 5 \mu$); membrane densely granular.

Exine max. 2μ thick at poles, 5μ at equator. Sexine 1μ thick at poles, 3μ at equator, punctitegillate. Tegillum less than 0.5μ thick, supported by densely spaced bacula. Big bacula densely spaced at the periphery, smaller bacula sparsely spaced in the "trema area". For nexine see p. 83.

There is a faint colpus-like depression ($25 \times 1.5 \mu$) in each "trema area" (it is either without processes or provided with very small processes).

Schaueria calicotricha Nees (cult. Lund): 3-colporate (peritreme), prolate ($75 \times 53 \mu$).

Apocolpium diameter about 35μ . Colpi about $54 \times 10 \mu$, with tapering ends; membrane faintly granular at the margins, densely granular in the centre. Ora lolongate (about $7 \times 5 \mu$). Each mesocolpium provided with two long, narrow, colpoid streaks (about $55 \times 1 \mu$), about 8μ sideways from equator.

Exine about 3μ thick. Sexine 1.5μ thick, reticulate (ectosexine less than 0.5μ thick). Nexine, as it seems, consists of two layers, ecto- and endonexine (inner surface of endonexine uneven).

Reticulum homobrochate. Muri straight, about 1μ wide, simplibaculate. Lumina hexagonal to circular (maximum diameter about 2.5μ).

Polytrema vulgare C.B. Cl. (Indo-China; Squires 806): irregularly 6-colporate or polycolporate (peritreme), spheroidal (about 44μ). Colpi about $40 \times 3 \mu$, with tapering ends. Ora slightly lolongate (about $5 \times 4 \mu$). Each mesocolpium provided with two long, narrow, colpoid streaks (about $40 \times 1 \mu$), about 4μ sideways from colpi.

Exine about 3μ thick. Sexine about 1μ thick, fragmentimurate. "Muri" less than 1μ wide. Nexine, as it seems, consists of two layers, ecto- and endonexine.

Rhinacanthus communis Nees (Natal; Ward 322): 3-colporate (pleurotreme), prolate ($52 \times 36 \mu$).

Apocolpium diameter about 12μ . Colpi about $50 \times 3 \mu$. Ora lolongate (about $5 \times 3 \mu$). Each mesocolpium provided with two long, narrow, colpoid streaks, about 5μ sideways from colpi.

Exine about 6μ thick. Sexine about 3μ thick, reticulate in apocolpia and streaks along colpi margins, otherwise punctitegillate. Tegillum about 1μ thick. Nexine, as it seems, consists of two layers, ecto- and endonexine.

R. nasutus (L.) Lindau (Siam; Zimmermann 72): 3-colporate, prolate ($50 \times 30 \mu$).

Thysacanthus callistachyus Nees (Mexico; Fröderström & Hultén 1054): 4-colporate, prolate ($60 \times 40 \mu$).

T. strictus Nees (cult. N.Y. Bot. Garden): 4-colporate (occasionally 5-, rarely 6- or more), peritreme, spheroidal (about 65μ).

Apocolpium diameter about 40μ . Colpi about $40 \times 3 \mu$, with ta-

pering ends; membrane faintly granular. Ora lolongate (about $10 \times 6 \mu$). Each mesocolpium provided with two colpoid streaks (about $45 \times 1-2.5 \mu$), about 5μ sideways from colpi.

Exine about 3μ thick. Sexine about 1μ thick, reticulate (ectosexine less than 0.5μ). Nexine, as it seems, consists of two layers, ecto- and endonexine.

Reticulum homobrochate. Muri straight, less than 0.5μ wide, simplibaculate. Lumina polygonal to circular (maximum diameter about 1.5μ).

RHYTIGLOSSEAE

Kalbreyerella rostellata Lindau (Colombia; Lawrence 694). Pl. 17, Figs. 1-4.—Pollen grains 2-porate, spheroidal (diameter about 77μ). Pores circular (about 10μ). Region around pores densely spaced with small processes.

Exine (suprategillar processes not included) 3μ thick. Sexine about 1μ thick, tectate (usually thicker and sometimes intectate in a belt halfway between pores). Tegillum less than 0.5μ thick, supported by bacula (about 0.5μ long) and provided with $4-7 \mu$ long, blunt, solid spines.

Fittonia verschaffeltii E. Coem. (cult. Hort. Berg.): 3-porate, spheroidal (diameter about 34μ). Pores more or less circular (about 5μ); membrane densely granular.

Exine about 3μ thick. Sexine about 1μ thick, suprareticulate (ectosexine as thick as endosexine, punctate, undulating). Nexine, as it seems, consists of two layers, ecto- and endonexine.

Reticulation "homobrochate". Muroid ridges winding, about $0.5-1 \mu$ wide. Luminoid areas polygonal to circular (maximum diameter about $1-2 \mu$). Pollen grains very variable.

Poikilacanthus gilliesii Lindau (Uruguay; Lorentz 512). Pl. 22, Figs. 1-4.—Pollen grains polyporate (6-12 or more), prolate (about $61 \times 45 \mu$). Pores circular (about 3μ); membrane granular.

Exine 5μ thick. Sexine 2μ thick, made up of regularly arranged, polygonal insulae consisting of densely spaced, small processes held together by a solid marginal belt. Average diameter of insulae about 5μ . Nexine consists of ecto- and endonexine.

Rhacodiscus calycinus (Nees) Brem. (Brit. Guiana; Maguire & Fanshawe 22919). Pl. 24, Figs. 1-4.—Pollen grains 2-porate, bilateral ($65 \times 36 \times ? \mu$). Pores circular to lalongate (about $3 \times 5 \mu$); membrane densely granular.

Exine (suprattegillar processes included) about $4\ \mu$ thick at poles, $3\ \mu$ at equator. Sexine about $2\ \mu$ thick at poles, $4\ \mu$ at equator, tectate. Tegillum less than $0.5\ \mu$ thick in "peripheral area", supported by densely spaced, slender bacula; its general surface uneven. Verrucae about $2 \times 4\ \mu$, with a small spherical or transversely elongated hollow. Nexine, as it seems, consists of two layers, ecto- and endonexine.

Rhytiglossa lactea (Lindau) ex Engl. (Nyasa; Stoltz 2177). Pl. 16, Figs. 1-3.—Pollen grains 2-porate, "bilateral" ($40 \times 40 \times 22\ \mu$). Pores more or less circular (about $5\ \mu$); membrane granular (granules about $1-2\ \mu$).

Exine up to $7\ \mu$ thick. Sexine up to $6\ \mu$ thick, punctitiegillate. Tegillum almost smooth, about $1.5\ \mu$ thick; it appears to be formed by the partial amalgamation of much branched bacula. Nexine incrassate at pores; it consists, as it seems, of two layers, ecto- and endonexine.

Brachystephanus africanus S. Moore (Uganda; Purseglove 3309). Pl. 8, Figs. 1-4.—Pollen grains 3-porate (occasionally tetraporate), spheroidal (diameter about $56\ \mu$). Pores circular to slightly elongate (olongate—about $10 \times 6\ \mu$); membrane granular.

Exine (suprattegillar processes not included) $4\ \mu$ thick. Sexine $1-3\ \mu$ thick, tectate. Tegillum less than $0.5\ \mu$ thick.

Exine with three band-shaped "mesocolpial" depressions, about $3\ \mu$ wide, anastomosing at the poles. The depressions as well as the areas between them are provided with verrucae (about $1\ \mu$ high) and smaller baculoid processes. The latter are larger and more densely spaced in the depressions than on the rest of the surface. Nexine, as it seems, consists of a single, homogeneous layer.

Habracanthus sylvaticus Nees (Mexico; Mexia 9273): 2-porate, bilateral ($37 \times 37 \times 25\ \mu$). Pores more or less circular (about $5\ \mu$); membrane densely granular. The areas (diameter about $20\ \mu$) surrounding the apertures are provided with densely spaced, circular insulae (diameter about $1-3\ \mu$).

Exine about $4\ \mu$ thick. Sexine about $3\ \mu$ thick, tectate. Tegillum about $2\ \mu$ thick, smooth, supported by slender bacula. Nexine, as it seems, consists of two layers, ecto- and endonexine (inner surface of endonexine uneven).

Glockeria gracilis Nees (Mexico; Bourgeau 2000). Pl. 13, Figs. 1-7.—Pollen grains 2-porate, spheroidal (diameter about $45\ \mu$). Pores circular or slightly lologate (about $7 \times 5\ \mu$); membrane granular.

Exine (supratégillar processes not included) about $6\ \mu$ thick. Sexine less than $1\ \mu$ thick, tectate. Tegillum less than $0.5\ \mu$ thick, supported by about $0.5\ \mu$ long bacula and provided with $2\ \mu$ long, sparsely spaced, blunt, solid spinules.

Exine (in pollen grains seen in polar view) between the pores forms a concavity in the centre and is in continuation with a colpoid streak (about $4\ \mu$ wide), which divides the grain into two hemispherical areas. The colpoid streak, which is slightly depressed, has big bacula and a few scattered spinules. Nexine, as it seems, consists of a single, homogeneous layer.

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Chaetothylax umbrosus Nees (Argentina; Willink 221): 2-porate (occasionally there is an indication of a faint colpus at each aperture), bilateral ($49 \times 39 \times 22\ \mu$). Pores lalongate (about $2 \times 4\ \mu$). "Trema area" studded with more or less circular insulae (about $5-6\ \mu$) with a very fine pattern.

Exine up to $5\ \mu$ thick. Sexine about $3\ \mu$ thick, tectate. Ectosexine undulating, appearing as a reticulate, "homobrochate" pattern. Muroid ridges winding, about $0.5\ \mu$ wide. Luminoid areas polygonal (maximum diameter about $1\ \mu$).

Dianthera ciliata Benth. & Hook. f. (cult. N.Y. Bot. Garden): 2-porate, bilateral ($64 \times 40 \times 32\ \mu$).

D. collina C.B. Cl. (India; Chatterjee 183): 2-porate, spheroidal (diameter about $50\ \mu$).

D. comata L. (Guatemala; von Türckheim 4135): 3-colporate (pleurotreme), subprolate ($28 \times 22\ \mu$).

Apocolpium diameter about $12\ \mu$. Colpi about $18 \times 3\ \mu$, with tapering ends. Ora lalongate (about $2 \times 3\ \mu$). Each mesocolpium provided with two long, narrow, colpoid streaks (about $9 \times 1\ \mu$).

Exine about $4\ \mu$ thick. Sexine about $3\ \mu$ thick, tectate (ectosexine undulating and appears to be formed by the partial amalgamation of the upper part of funnel-shaped bacula). Bacula bases free, forming a supporting layer. Nexine, as it seems, consists of two layers, ecto- and endonexine.

Jacobinia aurea Hemsl. (Mexico; Pringle 4865): 2-porate (occasionally there is an indication of a faint colpus at each aperture), bilateral ($77 \times 53 \times ?\ \mu$). Pores slightly lalongate (about $3 \times 4\ \mu$).

Exine about $4\ \mu$ thick at poles, up to $7\ \mu$ at equator. Sexine about $2\ \mu$ thick at poles, up to $5\ \mu$ at equator, tectate. Tegillum

about $1\ \mu$ thick, undulating and appears to be formed by the partial amalgamation of apically much branched bacula.

"Trema area" studded with finely patterned, more or less circular insulae (maximum diameter about $4\ \mu$). The nexine consists of two distinct layers (ecto- and endonexine).

J. carnea (Lindl.) Nichols. (Rio de Janeiro; Erdtman). Pl. 10, Figs. 4-7.—Pollen grains 2-porate (occasionally there is an indication of a faint colpus at each aperture), bilateral ($82 \times 50 \times ?\ \mu$). Pores circular (about $4\ \mu$); membrane sparsely granular.

Exine about $3\ \mu$ thick at poles, up to $6.5\ \mu$ at equator. Sexine about $1\ \mu$ thick at poles, up to $2\ \mu$ at equator, tectate. Tegillum $1-2\ \mu$ thick, psilate, supported by bacula (much branched at apex).

"Trema area" ($40 \times 20\ \mu$) studded with finely patterned insulae (diameter about $1-2\ \mu$). For nexine see p. 83.

J. carnea (Lindl.) Nichols. Pl. 16, Figs. 4-8. The pollen grains (from Hort. Berg.) are only slightly different from those of the above.

J. chrysostephana Benth. & Hook. f. (cult. N.Y. Bot. Garden): 3-porate, prolate ($68 \times 46\ \mu$). Each mesocolpium provided with two colpoid streaks.

J. coccinea Hiern (herb. Mus. Bot. Ups.): 3(4)-porate, prolate ($60 \times 38\ \mu$).

J. pauciflora Benth. & Hook. f. (cult. Lund): 2-porate, bilateral ($70 \times 43 \times 32\ \mu$).

J. tenuistachys Rusby (Bolivia; Bang 1441): 2-porate, bilateral ($38 \times 26 \times 20\ \mu$). Pores lalongate (about $4 \times 5\ \mu$); membrane sparsely granular.

Exine up to $2\ \mu$ thick at poles, up to $5\ \mu$ at equator. Sexine $1\ \mu$ thick at poles, $3\ \mu$ at equator, punctitegillate in the "peripheral area". Tegillum about $1\ \mu$ thick, supported by bacula (branched at apex).

"Trema area" longitudinal ($35 \times 10\ \mu$) beset with more or less circular, finely reticulate insulae (diameter about $1-2\ \mu$). Nexine, as it seems, consists of two layers, ecto- and endonexine.

Beloperone californica Benth. (California; Rose 59006). Pl. 6, Figs. 6-9.—Pollen grains 2-porate (occasionally there is an indication of a faint colpus at each aperture), bilateral ($75 \times 50 \times 40\ \mu$). Pores lalongate (about $3 \times 6\ \mu$); membrane sparsely granular.

Exine $3\ \mu$ thick at poles, $4\ \mu$ at equator. Sexine $2\ \mu$ thick at poles, $3\ \mu$ at equator, punctitegillate. Tegillum supported by bacula (bacula much branched at apex).

"Trema area" longitudinal ($60 \times 15 \mu$) studded with circular insulae (about 5μ), which coalesce at the poles. Nexine, as it seems, consists of two layers, ecto- and endonexine.

B. plumbaginifolia Nees (cult. Rio de Janeiro): 2-porate, bilateral ($74 \times 45 \times 35 \mu$).

B. ramulosa Morong (Paraguay; Balansa 3296): 2-porate, bilateral ($61 \times 46 \times 40 \mu$).

B. scorpioides Nees (Argentina; Lorentz & Hieronymus 226): 2-porate, bilateral ($70 \times 40 \times 37 \mu$).

Dasytropis fragilis Urb. (Cuba; Ekman 15236): 4-colporate (peritreme), subprolate to prolate ($50 \times 36 \mu$).

Apocolpium diameter about 15μ . Colpi about $42 \times 2-10 \mu$, with tapering ends. Ora lalongate (about $5 \times 10 \mu$).

Exine about 4μ thick at poles, 5μ at centre of mesocolpia. Sexine about 1μ thick at poles, 2μ at centre of mesocolpia.

Lateral parts of mesocolpia finely reticulate, occasionally provided with two colpoid streaks (about $40 \times 2-3 \mu$), central part punctitegillate. Tegillum less than 0.5μ , smooth and appears to be formed by the amalgamation of much branched bacula. Nexine, as it seems, consists of two layers, ecto- and endonexine.

Drejerella guttata (Brdge.) Brem. (cult. Copenhagen): 3-porate, prolate ($67 \times 42 \mu$). For nexine see p. 83.

Justicia adhatoda Nees (Hong Kong): 2-porate, bilateral ($66 \times 47 \times 40 \mu$).

J. championi T. And. ex Benth. (Hong Kong): 2-porate, bilateral ($40 \times 30 \times ? \mu$).

J. debilis Lam. (Tanganyika; Lambert 11): 2-porate, bilateral ($50 \times 32 \times 27 \mu$).

J. divaricata C.B. Cl. (Natal; Rogers 3): 2-porate (there is an indication of a colpus at each aperture, about $20 \times 1 \mu$), bilateral ($40 \times 26 \times 16 \mu$). Pores lalongate (about $3 \times 5 \mu$); membrane densely granular.

Exine about 3μ thick at poles, 4μ at equator. Sexine 2μ thick at poles, 2μ at equator.

"Trema area" provided with more or less circular insulae (about 2.5μ), with a reticulate pattern. "Peripheral area" punctitegillate. Tegillum about 2μ thick, undulating; it appears to be formed by partial amalgamation of much branched bacula (their bases free, forming a supporting layer). Nexine, as it seems, consists of two layers, ecto- and endonexine.

J. gendarussa Burm. (India): 3-colporate (pleurotreme), prolate ($36 \times 23 \mu$). One grain with 3 colpi but only 2 ora seen.

Apocolpium diameter about 6μ . Colpi about $30 \times 1 \mu$, with tapering ends; membrane sparsely granular. Ora lalongate (about $2 \times 3 \mu$).

Exine 4μ thick. Sexine about 2μ thick, tectate. Tegillum less than 0.5μ thick, smooth. For nexine see p. 84.

J. hyssopifolia L. (cult. Canary Islands; Sventenius): 2-porate, bilateral ($63 \times 52 \times 35 \mu$). Pores lalongate ($4 \times 7 \mu$); membrane granular.

Exine 4μ thick at poles, 8μ at equator. Sexine 3μ thick at poles, 5μ at equator, tectate. Tegillum supported by densely spaced bacula. Bacula in the "trema area" smaller than in the "peripheral area". Nexine, as it seems, consists of two layers, ecto- and endonexine.

"Trema area" with two long, narrow, tapering, colpoid streaks ($63 \times 4 \mu$). Narrow, colpus-like slits present above and below the apertures.

J. laevilinguis (Nees) Lindau (Buenos Aires; Lillo 53): 2-porate, bilateral ($49 \times 37 \times 28 \mu$). Pores lalongate (about $3 \times 5 \mu$); membrane densely granular.

Exine 4μ thick at poles, 7μ at equator. Sexine 3μ thick at poles, 5μ at equator, tectate. Tegillum supported by bacula. Nexine, as it seems, consists of two layers, ecto- and endonexine.

"Trema area" longitudinal (about $49 \times 15 \mu$), studded with ten or more reticulate insulae (diameter about $5 \times 3 \mu$) on either side of the apertures.

J. matammensis Oliver (Nairobi; Verdcourt): 2-porate, bilateral ($22 \times 16 \times 12 \mu$). Pores circular (about 3μ); membrane sparsely granular.

Exine 2μ thick at poles, up to 3μ at equator. Sexine 1μ thick at poles, 2μ at equator, partially tectate. Nexine, as it seems, consists of two layers, ecto- and endonexine.

"Trema area" longitudinal ($20 \times 15 \mu$), studded with eight or more circular insulae (diameter about 3μ). Insulae reticulate; they are slightly elongated and finally coalesce towards the pores.

J. natalensis T. And. (Natal; "Stellenbosch 2691"): 3-colporate (pleurotreme), prolate ($50 \times 34 \mu$).

Apocolpium diameter about 26μ . Colpi about $35 \times 3 \mu$, with tapering ends; membrane densely granular (granules about 2μ). Ora

lalongate (about $5 \times 9 \mu$). Each mesocolpium provided with two long, narrow, colpoid streaks (about $32 \times 1-3 \mu$).

Exine about 2μ thick at poles, 4μ at centre of mesocolpia. Sexine 1μ thick punctitegillate in the "peripheral area", reticulate in the "trema area". Muri and lumina less than 0.5μ wide. Tegillum less than 0.5μ thick at poles, about 0.5μ at centre of mesocolpia, supported by stout bacula. Nexine, as it seems, consists of two layers, ecto- and endonexine.

J. platycarpa Lillo (Argentina; Erdtman): 2-porate, bilateral (about $51 \times 35 \times 26 \mu$). Pores lalongate ($3 \times 5 \mu$); membrane sparsely granular.

Exine 3μ thick at poles, 5μ at equator. Sexine 1.5μ thick at poles, 3.5μ at equator, punctitegillate in "peripheral area". "Trema areas" longitudinal ($40 \times 15 \mu$), studded with circular, finely reticulate insulae (diameter about 4μ). For nexine see p. 84.

J. procumbens L. (China; Tsang 21689): 2-porate, bilateral ($32 \times 22 \times ? \mu$). Pores circular (about 2μ); membrane sparsely granular. Each "mesocolpium" provided with a narrow, colpoid streak.

Exine 4μ thick at poles, 7μ at equator. Sexine 2μ thick at poles, 5μ at equator, tectate (punctitegillate ?) in "peripheral area". Tegillum supported by densely spaced, slender bacula.

"Trema area" longitudinal ($30 \times 15 \mu$), studded with more or less circular insulae (diameter about 2μ). Insulae reticulate; they coalesce towards the poles. Nexine, as it seems, consists of two layers, ecto- and endonexine.

J. ventricosa Wall. (Hong Kong, anno 1950): 3-colporate (occasionally 2-porate; there is an indication of a faint colpus at each aperture), prolate ($55 \times 35 \mu$).

Apocolpium diameter about 18μ . Colpi about $48 \times 2 \mu$, with tapering ends; membrane faintly granular. Ora lalongate ($3 \times 4 \mu$). Each mesocolpium provided with two colpoid streaks ($45 \times 2 \mu$).

Exine 4μ thick. Sexine 2μ thick, tectate (punctitegillate ?). Tegillum less than 0.5μ thick, supported by bacula (bacula much branched at apex). Bacula in "trema area" slightly smaller than those in the "peripheral area". Nexine, as it seems, consists of two layers, ecto- and endonexine.

Duvernoya adhatodoides E. Mey. (Africa): 2-porate (there is an indication of a colpus about $45 \times 3 \mu$ at each aperture), bilateral ($65 \times 43 \times ? \mu$). Pores circular (about 4μ). Each "mesocolpium" provided with two faint colpoid streaks.

Exine about $4\ \mu$ thick at poles, $9\ \mu$ at equator. Sexine $2\ \mu$ thick at poles, up to $5\ \mu$ at equator, reticulate in the "trema area", punctitegillate in the "peripheral area". Tegillum about $0.5\ \mu$ thick at poles, $3\ \mu$ at equator, supported by bacula (probably branched at the apex). Nexine, as it seems, consists of two layers, ecto- and endonexine.

Adhatoda schimperiana Hochst. ex Nees (Kenya; Drummond & Hemsley 4119): 2-porate (occasionally there is an indication of a faint colpus at each aperture), bilateral ($70 \times 45 \times 42\ \mu$). Pores lalongate ($4 \times 6\ \mu$); membrane densely granular; margin of pores beset with very small processes.

Exine up to $5\ \mu$ thick at poles, $8\ \mu$ at equator. Sexine $2\ \mu$ thick at poles, $5\ \mu$ at equator, gradually thinner towards the poles, punctitegillate in the "peripheral area", beset with more or less circular insulae (with a finely reticulate pattern) in the "trema area". Insulae slightly elongated and finally coalesce towards the poles. Nexine, as it seems, consists of two layers, ecto- and endonexine.

A. vasica Nees (India, Hyderabad; Saxena): 2-porate (occasionally there is an indication of a faint colpus at each aperture), bilateral ($60 \times 42 \times 36\ \mu$). Pores lalongate ($4 \times 6\ \mu$); membrane sparsely granular (granules about $2-3\ \mu$); margin of pores beset with very small processes.

Exine about $5\ \mu$ thick. Sexine about $2\ \mu$ thick, punctitegillate in the "peripheral area", finely reticulate in the "trema area". Tegillum about $1.5\ \mu$ thick, sharply undulating in "peripheral area". "Trema area" occasionally broken up into more or less circular insulae. For nexine see p. 80.

Pedaliaceae

Pedalium murex L. (Madagascar; Perrier 1275): 6-colpate (peritreme), oblate ($55 \times 90\ \mu$).

Apocolpium diameter about $32\ \mu$. Colpi about $52\ \mu$.

Exine about $3\ \mu$ thick. Sexine about $1\ \mu$ thick, finely reticulate (ectosexine as thick as endosexine, smooth). Nexine, as it seems, consists of a homogeneous layer.

Reticulum homobrochate. Muri more or less straight, about $0.5\ \mu$ wide, simplibaculate. Lumina polygonal (maximum diameter about $0.5\ \mu$).

Pterodiscus angustifolius Engl. (Tanganyika; Burt 6430): 5-7-colpate (peritreme), oblate ($47 \times 67 \mu$).

Apocolpium diameter about 35μ . Colpi about $35 \times 3 \mu$; membrane densely granular.

Exine about 4μ thick. Sexine about 2μ thick at poles and 3μ at centre of mesocolpia, finely reticulate (ectosexine about 0.5μ thick, smooth). Nexine, as it seems, consists of a homogeneous layer.

Reticulum homobrochate. Muri more or less straight, about 0.5μ wide, simplibaculate. Lumina punctoid (maximum diameter about 0.5μ), spaced about $1-1.5 \mu$ apart. Nexinous cracks (often pairwise at right angles to colpi).

Harpagophytum procumbens DC. (S. Africa; Bolus): 7(-8)-colpate (peritreme), subprolate ($67 \times 55 \mu$).

Apocolpium diameter about 20μ . Colpi about $52 \times 2-4 \mu$, with tapering ends, tenuimarginate; membrane densely granular.

Exine about 4μ thick. Sexine about 1μ thick at poles and 3μ at centre of mesocolpia, tectate. Tegillum at centre of mesocolpia about 2μ thick, psilate; it appears to be formed by the amalgamation of densely spaced, slender bacula. Nexine incrassate at poles; cracks much as in *Pterodiscus*.

Holubia saccata Oliv. (S. Africa; Rogers 3105): 5-7-colpate (colporate?), peritreme, spheroidal (about 70μ).

Apocolpium diameter about 36μ . Colpi tenuimarginate; membrane slightly granular.

Exine about 4μ thick. Sexine about 3μ thick, finely reticulate (ectosexine about 0.5μ thick, slightly undulating; endosexine densely baculate).

Reticulum homobrochate. Muri about 0.5μ wide, cf. simplibaculate. Lumina more or less polygonal (maximum diameter about 0.5μ).

Uncarina aff. *didieri* (Baill.) Stapf (Madagascar; Kaudern s.n.): 5-colporoidate (partially parasyncolpate), peritreme, prolate spheroidal ($67 \times 59 \mu$).

Apocolpium diameter about 22μ ; its amb polygonal. Colpi about $60 \times 1-3 \mu$, with tapering or rounded ends; membrane smooth. Oroids $16 \times 14 \mu$.

Exine about 4μ thick. Sexine 3μ thick, reticulate (ectosexine about 1μ thick, smooth).

Rogersia adenophylla J. Gay (Angola; Fritzsche 176): 8-colpate

(faintly parasyncolpate, peritreme), prolate spheroidal ($67 \times 59 \mu$).

Apocolpium diameter about 20μ .

Exine about 3μ thick. Sexine about 1μ thick at poles and 2μ at centre of mesocolpia, tectate (ectosexine as thick as endosexine at poles and slightly thicker at centre of mesocolpia, undulating). Nexine, as it seems, consists of a thin, homogeneous layer.

Tegillum punctate. Supporting bacula large, very densely spaced. Puncta polygonal to circular (maximum diameter about 1μ).

Sesamum angustifolium Engl. (Dybowski 156): 7(-8)-colpate (peritreme), prolate spheroidal-subprolate ($57 \times 50 \mu$).

Apocolpium diameter about 23μ . Colpi about $36 \times 2 \mu$, tenuimarginate; membrane densely granular.

Exine $4-6.5 \mu$ thick. Sexine about 2μ thick at poles and 4μ at centre of mesocolpia, made up of piloid processes densely studded on a layer built up of granular, vertical streaks. Nexine homogeneous, incrassate in apocolpia.

S. capense Burm. (S. Africa; Örtendahl 101): 6-colpate, parasyncolpate (peritreme), subprolate ($75 \times 62 \mu$).

Apocolpium diameter about 13μ . Colpi about $50 \times 2-5 \mu$, with tapering ends, tenuimarginate; membrane densely granular.

Exine about 5μ thick. Sexine 2μ thick at poles, 4μ at centre of mesocolpia, made up of piloid processes (a big pilum surrounded by a few small pila), and supported by a thin layer made up of thin, vertical rods. Nexine, as it seems, consists of a homogeneous layer.

S. indicum L. (Argentina; Ekman 1794): 9-11-colpate (peritreme), oblate (about $41 \times 60 \mu$).

Apocolpium diameter about 30μ . Colpi about $38 \times 1-4 \mu$, tenuimarginate.

Exine about 5μ thick. Sexine about 2μ thick at poles, 4μ at centre of mesocolpia, made up of piloid processes densely studded on a layer built up of small granules. Granules less densely spaced at the base. Nexine, as it seems, consists of a homogeneous layer. See also p. 88.

Ceratotheca triloba E. Mey. ex Bernh. (Natal; E. Wall s.n.): 8-9-colpate (peritreme), subprolate ($62 \times 50 \mu$).

Apocolpium diameter about 22μ . Colpi about $30 \times 2-4 \mu$, tenuimarginate; membrane densely granular.

Exine about 5μ thick. Sexine about 2μ thick at poles, 4μ at centre of mesocolpia, made up of piloid processes densely studded

on a granular layer. Granules less densely spaced at the base, forming a weak zone. Nexine, as it seems, consists of a homogeneous layer.

Linariopsis prostrata Welw. (Angola; Welwitsch 1659): (9-)10(-11)-colpate (-colporate), peritreme, subprolate ($52 \times 61 \mu$).

Apocolpium diameter about 24μ . Colpi about $37 \times 4 \mu$, with tapering ends, tenuimarginate. Ora faintly marked, circular (diameter about 5μ).

Exine about 6μ thick. Sexine about 3μ thick at poles, 5μ at centre of mesocolpia, made up of pila (about 1μ high) densely studded on a layer (about 2μ thick), built up of slender, vertical, granular rods. Granules less densely spaced at the base, forming a weak zone. Nexine, as it seems, consists of a homogeneous layer.

Pretrea zanguebarica J. Gay (Transvaal): 8-colpate (peritreme), oblate spheroidal ($54 \times 57 \mu$).

Apocolpium diameter about 15μ . Colpi about $45 \times 4 \mu$, tenuimarginate.

Exine about 6μ thick. Sexine about 2μ thick at poles, 4μ at centre of mesocolpia, made up of piloid processes densely studded on a layer which appears more or less compact. Below this is another thin layer which appears to be made up of very thin, vertical rods. Nexine, as it seems, consists of a homogeneous layer.

Josephinia africana Vatke (Kenya; Gillet 15150): 7-8-colpate (peritreme), subprolate ($41 \times 47 \mu$).

Apocolpium diameter about 20μ . Colpi about $35 \times 4 \mu$, with tapering ends, tenuimarginate; membrane densely granular (granules about 1μ).

Exine about 5μ thick. Sexine about 2μ thick at poles, 4μ at centre of mesocolpia, tectate. Tegillum undulating formed by the amalgamation of densely spaced, slender bacula, their bases remaining free to appear as a thin, supporting baculate layer. Nexine, as it seems, consists of a homogeneous layer.

Niedzwedzkia semiretschenskia B. Fedtsch. (Tianschan; Joffe & Titov): 6(-7)-colpate (peritreme), prolate spheroidal ($49 \times 43 \mu$).

Apocolpium diameter about 22μ . Colpi about $38 \times 3-5 \mu$, with tapering ends; membrane granular.

Exine about 2μ thick. Sexine about 1μ thick, tectate. Tegillum about 0.5μ thick, slightly wavy. Nexine, as it seems, consists of a homogeneous layer.

Discussion of morphological features

Probably no other family has such a wide range of pollen-morphological features as the Acanthaceae. Out of the 260 species investigated, *Staurogyne diantheroides*, *Monothecium aristatum*, *Nelsonia canescens*, etc. have the smallest grains, while *Acanthopale* sp. (Pl. 1, Figs. 1-4), *Barleria courtallica* (Pl. 39, Fig. 2), *Louteridium donnell-smithii* (Pl. 19, Figs. 1-3), etc. have the largest. The length of the polar axis ranges from 20 μ , as in *Staurogyne diantheroides*, to 140 μ as in *Louteridium donnell-smithii*.

The shape of the grains varies from peroblate, as in *Meyenia hawtayneana* (Pl. 21, Figs. 1-4) to perprolate, as in *Aphelandra lutea*, *Crossandra undulaefolia*, *Dicliptera niederleiniana* and *Geisomeria tetragona* (Pl. 12, Figs. 5-8).

With regard to the apertures most of the nomotreme pollen types are monozonotreme: colpate, as in *Acanthus ilicifolius* (Pl. 3, Fig. 4); colporate, as in *Rhinacanthus communis*; porate, as in *Ruellia capitata* (3 pores) and *Poikilacanthus gilliesii* (12 pores; Pl. 22, Figs. 1-4); rarely irregularly monozonotreme, as in *Brillantaisia emini* (Pl. 9, Fig. 4). Some pollen types are pantotreme, e.g. pantoporate as in *Louteridium donnell-smithii* and *Acanthopale* sp. There are also anomotreme grains, e.g. in *Stenandrium trinerve* (Pl. 29, Figs. 8-11) and in *Thunbergia fragrans* and *Pseudocalyx africanus* (Pl. 23, Figs. 1-4).

In all grains investigated, the colpi are broadest in the middle and tapering at both ends, except in *Acanthus dioscoridis*, where they are not tapering, and in *Odontonema callistachyum* and *Andrographis echinoides* where they often have an equatorial constriction.

The colpi are short, narrow and slit-like, e.g. in *Mendoncia aspera* (Pl. 20, Fig. 4) and *Monachochlamys flagellaris*, more open in *Codonacanthus pauciflorus*.

The grains of *Blechum brownei* (Pl. 7, Figs. 1-4) and *B. laxiflorum* are syncolpate.

Colpoid streaks are met with, e.g. in *Asteracantha longifolia*, *Asystasia coromandeliana* (Pl. 5, Figs. 1-4), *Mellera lobulata* (Pl. 20, Figs. 1, 2) and *Ruttya ovata*.

In *Stenosiphonium russelianum* the colpoid streaks are not straight, in *Aechmanthera gossypina*, *Brillantaisia emini*, *Ruttya ovata*, *Asteracantha longifolia*, *Hypoestes antennifera* (Pl. 15, Figs.

1-4) and *Justicia hyssopifolia*, etc., they are longitudinal, long and narrow and of the same length as the real apertures. In *Calophanes ciliatus*, *C. persoonii*, *Petalidium barlerioides*, *Hygrophila bayatensis* and *Phaylopsis dorsiflora*, etc., they are also longitudinal and narrow but longer than the apertures. In *Monothecium aristatum* and *Ballochia amoena* the colpoid streaks are longitudinal and narrow but shorter than the apertures.

In *Brachystephanus africanus* (Pl. 8, Figs. 1-3) and *Glockeria gracilis* (Pl. 13, Figs. 1-3) the colpoid streaks are broad and band-shaped.

In *Dicliptera suberecta*, *Pseuderanthemum cuatrecasasii*, *Sympagis brunoniana* (Pl. 29, Figs. 12-13) and *Thyrsacanthus strictus*, the nonadjacent colpoid streaks anastomose in such a way that they form a circle between the apertures, whereas in *Graptophyllum insularum* the adjacent streaks anastomose in such a way that they encircle an aperture.

Yet another feature is the arrangement of the colpoid streaks in a manner so as to partially delimit two semicircular, sexinous patches, as seen in *Bravaisia floribunda*, *Mellera lobulata* (Pl. 20, Figs. 1, 2), *Petalidium barlerioides*, *Sanchezia klugii* (Pl. 28, Figs. 1-3), *Steirosanchezia scandens*, *Trichanthera gigantea*, etc. These, if arranged close to one another, give rise to a colporate condition with a narrow, slit-like colpus. The same patches, when wide apart, exhibit a typical porate condition.

Various patterns formed by fusion or division of colpoid streaks can be seen in *Asystasia coromandeliana*, *A. schimperi*, *Bravaisia floribunda*, *Sanchezia klugii* (Pl. 28, Figs. 1-3), etc.

The colpoid streaks hitherto mentioned can, at least in some cases, be compared with harmomegathi which, as described by Wodehouse (1935), are furrows accommodating semi-rigid exine to bring about a change in volume. If colpoid streaks with and without ora are to be grouped together, then the existing status of a colporate aperture will be reduced to a simple aperture enclosed in or surrounded by a colpoid streak.

In *Anisacanthus abditus*, *A. thurberi*, *Carlwrightia californica* (Pl. 40, Fig. 2), *Juruasia rotundata*, *Pachystachys riedeliana* and *Schaueria calicotricha* the grains are all provided with longitudinal, narrow, colpoid streaks as well as oriferous colpi showing different stages of expansion, from narrow to wide. In the wide open condition, the os is completely exposed, and in *Schaueria calicotricha*

there is even a thickening around the os as well as in the central, vertical zone of the colpus on either side of the os.

In *Andrographis echiioides* the grains are colporate without mesocolpial, colpoid streaks and the colpi range from equatorially constricted to fully expanded.

In *Beloperone californica*, *Jacobinia carnea*, *Ecbolium oreadam*, *Graptophyllum insularum*, *Justicia ventricosa*, *Peristrophe bivalvis* and *Pseuderanthemum cuatrecasasii*, etc. the colpi are very faintly marked (they merely appear as a slight depression).

In *Duvernaya adhatodoides*, *Ballochia amoena*, *Calophanes ciliatus*, *Dicliptera assurgens*, *D. scutellata*, *Justicia hyssopifolia*, *J. natalensis*, *Rhinacanthus communis*, *R. nasutus* and *Ruttya ovata* the faint colpi are discontinued at or near the ora and thus appear as meridional, non-equatorial depressions or folds.

Taking the above features into consideration, it would be more correct to restrict the description of apertures to that part of the apertures (in a wider sense) which actually can function as an opening. The enclosing colpoid streaks should perhaps be better described separately and not be included in the aperture proper.

The following table provides a summary of the main apertural features according to the 'NPC classification' (Erdtman and Straka 1961; see also Pl. 44 in this paper) as well as of the shape and size of the species investigated. These characteristics will be considered later in the taxonomical discussion (p. 92).

NPC Shape & size (↑ : bilateral grains)			NPC Shape & size		
<i>Nelsonioideae</i>			<i>Monachochlamys</i>		
<i>Staurogyne concinnula</i>	343	p. (32 × 22 μ)	<i>flagellaris</i>	445	p. sph. (45 × 42 μ)
<i>S. diantheroides</i>	343	p. (20 × 14.5 μ)	<i>Gilletiella congo-</i>	343 (443)	
<i>S. mandioccana</i>	343	p. (29 × 24 μ)	<i>lana</i>		p. sph. (27 × 25 μ)
<i>Elytraria imbricata</i>	343	p. (40 × 30 μ)	III. <i>Thunbergioideae</i>		
<i>E. tridentata</i>	343	p. (37 × 25 μ)	<i>Pounguia purpurata</i>	8	"sph." ("70 μ")
<i>Nelsonia canescens</i>	343	p. (25 × 15 μ)	<i>Meyenia hawtayne-</i>		
<i>Mendoncioideae</i>			<i>ana</i>	743	po. (31 × 65 μ)
<i>Mendoncia aspera</i>	545	p. sph. (51 × 47 μ)	<i>Thunbergia alata</i>	8	sph. (85 μ)
<i>M. breviflora</i>	645	p. sph. (45 × 40 μ)	<i>T. atriplicifolia</i>	8	sph. (85 μ)
<i>M. coccinea</i>	545	p. sph. (45 × 40 μ)	<i>T. coccinea</i>	8	sph. (70 μ)
<i>M. costaricana</i>	545	p. sph. (55 × 50 μ)	<i>T. erecta</i>	8	sph. (85 μ)
<i>M. lindavii</i>	545	p. sph. (55 × 50 μ)	<i>T. fragrans</i>	8	sph. (70 μ)
<i>M. schomburgkiana</i>	545	p. sph. (55 × 50 μ)	<i>T. friesii</i>	8	sph. (67 μ)

	NPC	Shape & size		NPC	Shape & size	
<i>T. gibsoni</i>	8	sph. (80 μ)	Petalidieae			
<i>T. grandiflora</i>	8	sph. (74 μ)	<i>Blechnum brownei</i>	345	sph. (47 μ)	
<i>T. laurifolia</i>	8	sph. (68 μ)	<i>B. laxiflorum</i>	345	ssph. (48 \times 46 μ)	
<i>T. mysorensis</i>	8	sph. (92 μ)	<i>Phaylopsis dorsi-</i>			
<i>T. sericea</i>	8	sph. (70 μ)	<i>flora</i>	345	p. (41 \times 28 μ)	
<i>T. venosa</i>	8	sph. (105 μ)	<i>P. longifolia</i>	345	p. (42 \times 28 μ)	
<i>T. vogeliana</i>	8	sph. (98 μ)	<i>P. oppositifolia</i>	345	sp. (44 \times 34 μ)	
<i>Pseudocalyx africa-</i>			<i>Petalidium barle-</i>			
<i>nus</i>	8	sph. (50 μ)	<i>rioides</i>	345	p. (70 \times 50 μ)	
<i>P. saccatus</i>	8	sph. (58 μ)	Strobilantheae			
IV. Acanthoideae						
Trichanthereae						
<i>Sanchezia arborea</i>	244 \uparrow	(92 \times 90 \times 80 μ)	<i>Calophanes amoenus</i>	345	p. (55 \times 40 μ)	
<i>S. filamentosa</i>	244 \uparrow	(82 \times 77 \times 65 μ)	<i>C. ciliatus</i>	345	p. (59 \times 36 μ)	
<i>S. klugii</i>	244 \uparrow	(70 \times 72 \times 60 μ)	<i>C. hygrophylloides</i>	345	p. (50 \times 36 μ)	
<i>S. loranthifolia</i>	244 \uparrow	(80 \times 75 \times 60 μ)	<i>C. maranhonis</i>	345	p. (60 \times 42 μ)	
<i>S. parvibracteata</i>	244 \uparrow	(107 \times 105 \times 95 μ)	<i>C. persoonii</i>	345	sp. (47 \times 38 μ)	
<i>S. peruviana</i>	244 \uparrow	(90 \times 84 \times 79 μ)	<i>C. repens</i>	345	p. (56 \times 35 μ)	
<i>S. stenantha</i>	244 \uparrow	(105 \times 92 \times 75 μ)	<i>Dyschoriste cuben-</i>			
<i>Steirosanchezia</i>			<i>sis</i>	345	p. (47 \times 28 μ)	
<i>scandens</i>	244 \uparrow	(92 \times 80 \times 72 μ)	<i>D. humilis</i>	345	sp. (55 \times 43 μ)	
<i>Bravaisia flori-</i>			<i>D. oaxacensis</i>	345	p. (53 \times 35 μ)	
<i>bunda</i>	244 \uparrow	(65 \times 62 \times 42 μ)	<i>Acanthopale sp.</i>	764	sph. (97 μ)	
<i>B. tubiflora</i>	244 \uparrow	(68 \times 65 \times 55 μ)	<i>Mimulopsis glandu-</i>			
<i>Trichanthera gigan-</i>			<i>losa</i>	345	p. (71 \times 52 μ)	
<i>tea</i>	244 \uparrow	(101 \times 96 \times 83 μ)	<i>Strobilanthes adna-</i>			
Louteridiaceae						
<i>Louteridium don-</i>			<i>tus</i>	345	p. (50 \times 30 μ)	
<i>nell-smithii</i>	764	sph. (140 μ)	<i>S. alatus</i>	345	p. (95 \times 60 μ)	
Hygrophileae						
<i>Mellera lobulata</i>	345	sp. (53 \times 40 μ)	<i>Sympagis bruno-</i>			
<i>Brillantaisia emini</i>	445	p.sph. (57 \times 52 μ)	<i>niana</i>	345	p.sph. (60 \times 55 μ)	
<i>B. lamium</i>	445	p.sph. (55 \times 50 μ)	<i>Stenosiphonium</i>			
<i>B. madagascari-</i>			<i>russelianum</i>	345	p. (60 \times 34 μ)	
<i>sis</i>	445	p.sph. (62 \times 60 μ)	<i>Aechmanthera gos-</i>			
<i>Asteracantha longi-</i>			<i>sykina</i>	345	p.-pp. (80 \times 40 μ)	
<i>folia</i>	445 \uparrow	(47 \times 52 \times 40 μ)	Haselhoffieae			
<i>Hygrophila angu-</i>			<i>Haselhoffia nema-</i>			
<i>stifolia</i>	345 (445)		<i>tosiphon</i>	343	p. (65 \times 45 μ)	
		p.sph. (35 \times 33 μ)	Ruellieae			
<i>H. bayatensis</i>	345	p. (55 \times 35 μ)	<i>Forsythiopsis ba-</i>			
<i>H. costata</i>	345	sp. (40 \times 34 μ)	<i>roni</i>	345	p. (60 \times 40 μ)	
<i>H. pringlei</i>	345	p. (62 \times 41 μ)	<i>Whitfieldia longi-</i>			
<i>H. spinosa</i>	345	p.sph. (70 \times 66 μ)	<i>folia</i>	764	sph. (70 μ)	
			<i>Eranthemum nervo-</i>			
			<i>sum</i>	344	sph. (105 μ)	
			<i>E. wattii</i>	344	sph. (100 μ)	
			<i>Ruellia acutangula</i>	344	sph. (65 μ)	
			<i>R. affinis</i>	344	sph. (64 μ)	

NPC Shape & size			NPC Shape & size		
<i>R. amoena</i>	344	sph. (61 μ)	<i>Acanthus arboreus</i>	343	pp. (46 \times 23 μ)
<i>R. angustiflora</i>	344	sph. (57 μ)	<i>A. dioscoridis</i>	343	pp. (57 \times 28 μ)
<i>R. bahiensis</i>	344	sph. (55 μ)	<i>A. hirsutus</i>	343	p. (58 \times 30 μ)
<i>R. baurii</i>	344	sph. (47 μ)	<i>A. hungaricus</i>	343	p. (53 \times 23 μ)
<i>R. brachysiphon</i>	344	sph. (83 μ)	<i>A. ilicifolius</i>	343	p. (54 \times 30 μ)
<i>R. capitata</i>	344	sph. (85 μ)	<i>A. leucostachyus</i>	343	pp. (53 \times 23 μ)
<i>R. formosa</i>	344	sph. (60 μ)	<i>A. longifolius</i>	343	p. (57 \times 32 μ)
<i>R. graecizans</i>	344	sph. (55 μ)	<i>A. syriacus</i>	343	pp. (56 \times 26 μ)
<i>R. hankeana</i>	344	sph. (70 μ)	<i>Crossandra green-</i>		
<i>R. harveyana</i>	344	sph. (72 μ)	<i>stockii</i>	343	pp. (48 \times 20 μ)
<i>R. hirsuta</i>	344	sph. (78 μ)	<i>C. nilotica</i>	343	p. (75 \times 40 μ)
<i>R. longifolia</i>	344	sph. (51 μ)	<i>C. undulaefolia</i>	343	pp. (80 \times 30 μ)
<i>R. neesiana</i>	344	sph. (99 μ)	<i>C. warneckii</i>	343	pp. (54 \times 23 μ)
<i>R. nitens</i>	344	sph. (87 μ)	<i>Sclerochiton boi-</i>		
<i>R. nudiflora</i>	344	sph. (55 μ)	<i>vini</i>	343	sp. (43 \times 34 μ)
<i>R. pacifica</i>	344	sph. (70 μ)	<i>S. harveyanus</i>	343	sp. (35 \times 27 μ)
<i>R. patula</i>	244 (344, 464 or 764)	sph. (52 μ)	Aphelandreae		
<i>R. portellae</i>	344	sph. (69 μ)	<i>Stenandrium bar-</i>		
<i>R. prostrata</i>	344	sph. (55 μ)	<i>batum</i>	343	p. (48 \times 30 μ)
<i>R. quadrifaria</i>	344	sph. (73 μ)	<i>S. droseroides</i>	343	p. (35 \times 20 μ)
<i>R. rubicaulis</i>	344	sph. (89 μ)	<i>S. pohlii</i>	764	sph. (40 μ)
<i>R. tessmannii</i>	344	sph. (89 μ)	<i>S. trinerve</i>	0	sph. (32 μ)
Barlerieae			<i>Geissomeria cin-</i>		
<i>Barleria courtallica</i>	344	sp. (127 \times 107 μ)	<i>cinnata</i>	343	pp. (69 \times 24 μ)
<i>B. lupulina</i>	344	sph. (102 μ)	<i>G. coccinea</i>	343	p. (65 \times 39 μ)
<i>B. noctiflora</i>	344	sph. (105 μ)	<i>G. longiflora</i>	343	pp. (66 \times 21 μ)
<i>B. prionitis</i>	344	sph. (90 μ)	<i>G. tetragona</i>	343	pp. (77 \times 30 μ)
<i>Barleriola multi-</i>			<i>Aphelandra acan-</i>		
<i>flora</i>	345	p. (72 \times 50 μ)	<i>thifolia</i>	343	pp. (66 \times 26 μ)
<i>B. solanifolia</i>	345	p. (41 \times 30 μ)	<i>A. acutifolia</i>	343 (443)	pp. (80 \times 45 μ)
<i>Crabbea acaulis</i>	244	sph. (57 μ)	<i>A. lineariloba</i>	343	p. (48 \times 27 μ)
<i>C. hirsuta</i>	244	sph. (60 μ)	<i>A. lutea</i>	343	pp. (77 \times 31 μ)
<i>Lepidagathis alo-</i>			<i>A. lyrata</i>	343	pp. (64 \times 23 μ)
<i>pecuroides</i>	345	p. (32 \times 22 μ)	<i>A. montisscalaris</i>	343	pp. (75 \times 28 μ)
<i>Lophostachys fal-</i>			<i>A. pulcherrima</i>	343	pp. (69 \times 25 μ)
<i>cata</i>	345	p. (65 \times 36 μ)	Rhombochlamydeae		
<i>L. floribunda</i>	345	p. (72 \times 42 μ)	<i>Rhombochlamys</i>		
<i>L. mufersa</i>	345	p. (45 \times 31 μ)	<i>elata</i>	343	p. (51 \times 30 μ)
Acantheae			<i>R. rosulata</i>	343	p. (50 \times 32 μ)
<i>Blepharis asper-</i>			Andrographideae		
<i>rima</i>	343	p. (42 \times 21 μ)	<i>Phlogacanthus cur-</i>		
<i>B. boerhaviaefolia</i>	343	p. (60 \times 30 μ)	<i>viflorus</i>	345	p. (48 \times 27 μ)
<i>B. edulis</i>	343	p. (40 \times 21 μ)	<i>P. pubinervius</i>	345	p. (46 \times 30 μ)
<i>B. molluginifolia</i>	343	p. (35 \times 20 μ)	<i>Andrographis echi-</i>		
			<i>oides</i>	345	p. (52 \times 36 μ)

	NPC	Shape & size		NPC	Shape & size
<i>A. paniculata</i>	345	p. (37 × 22 μ)	<i>Codonacanthus</i>		
<i>Cystacanthus turgidus</i>	345	p. (43 × 30 μ)	<i>pauciflorus</i>	445	so. (38 × 44 μ)
Asystasiaeae			<i>Ptyssiglottis parviflora</i>	345	p.sph. (45 × 40 μ)
<i>Thomandersia laurifolia</i>	543 (643)	o. (44 × 58 μ)	Odontonemeae		
<i>Chalarothyrsus amplexicaulis</i>	345	p. (62 × 40 μ)	<i>Ballochia amoena</i>	345	sph.-o.-sph. (47 × 48 μ)
<i>Spathacanthus hoffmanni</i>	345	sp. (71 × 60 μ)	<i>Ruttia ovata</i>	345	o.sph. (46 × 49 μ)
<i>Styasasia</i> sp.	544	sph. (50 μ)	<i>Monothecium aristatum</i>	345	sp. (25 × 20 μ)
<i>Asystasia bella</i>	344	p.sph. (59 × 56 μ)	<i>Hypoestes antennifera</i>	345	p. (61 × 38 μ)
<i>A. coromandeliana</i>	344	p. (87 × 48 μ)	<i>H. aristata</i>	345	p. (58 × 32 μ)
<i>A. gangetica</i>	344	p. (68 × 42 μ)	<i>H. verticillaris</i>	345	p. (44 × 25 μ)
<i>A. nemorum</i>	344	p. (65 × 41 μ)	<i>Peristrophe bivalvis</i>	345	sp. (61 × 51 μ)
<i>A. schimperii</i>	344	p. (59 × 40 μ)	<i>P. natalensis</i>	345	p. (54 × 35 μ)
<i>Chamaeranthemum beyrichii</i>	345	sp. (52 × 45 μ)	<i>P. speciosa</i>	345	p. (75 × 54 μ)
<i>Hulemacanthus whitei</i>	345	sp. (77 × 60 μ)	<i>Tetramerium glandulosum</i>	345	p. (45 × 27 μ)
Groptophylleae			<i>Rungia blumeana</i> var. <i>hirsuta</i>	244 ↑	(29 × 20 × 12 μ)
<i>Ruspolia decurrens</i>	345	p.sph. (59 × 52 μ)	<i>R. grandis</i>	244 ↑	(40 × 35 × 25 μ)
<i>Graptophyllum hortense</i>	345	p.sph. (70 × 62 μ)	<i>R. parviflora</i>	244 ↑	(longest axis about 30 μ)
<i>G. insularum</i>	344	sp. (55 × 46 μ)	<i>Dicliptera assurgens</i>	345	pp. (61 × 25 μ)
<i>G. pictum</i>	344	sp. (72 × 60 μ)	<i>D. chinensis</i>	345	p. (50 × 30 μ)
<i>Pachystachys lutea</i>	345	pp. (65 × 32 μ)	<i>D. heterostegia</i>	345	p. (55 × 37 μ)
<i>P. riedeliana</i>	345	p. (79 × 54 μ)	<i>D. niederleiniana</i>	345	p. (50 × 25 μ)
<i>Carlwrightia californica</i>	345	p. (38 × 25 μ)	<i>D. resupinata</i>	345	p. (50 × 25 μ)
<i>Anisacanthus abditus</i>	345	p. (55 × 34 μ)	<i>D. scutellata</i>	345	p. (57 × 32 μ)
<i>A. malmei</i>	345	sp. (43 × 37 μ)	<i>D. suberecta</i>	345	p. (67 × 42 μ)
<i>A. thurberi</i>	345	p. (77 × 53 μ)	<i>Juruasia rotundata</i>	345	sph. (44 μ)
<i>Thamnojusticia</i> sp.	244 ↑	(43 × 32 × 28 μ)	<i>Odontonema callistachyum</i>	345	sp. (51 × 41 μ)
<i>Chlamydocardia buettneri</i>	645	sph. (60 μ)	<i>Ecbolium oreadum</i>	244 ↑	(42 × 27 × 23 μ)
Pseuderanthemeae			<i>Schaueria calicotricha</i>	345	p. (75 × 53 μ)
<i>Pseuderanthemum cordatum</i>	345	p.sph. (45 × 42 μ)	<i>Polytrema vulgare</i>	645 (745)	sph. (44 μ)
<i>P. cuatrecasasii</i>	345	sp. (31 × 25 μ)	<i>Rhinacanthus communis</i>	345	p. (52 × 36 μ)
<i>P. malaccense</i>	345	p.sph. (52 × 48 μ)	<i>R. nasutus</i>	345	p. (50 × 30 μ)
<i>Mackaya bella</i>	345	p.sph. (50 × 48 μ)	<i>Thyrsacanthus callistachyus</i>	445	p. (60 × 40 μ)
<i>Sapphoa rigidifolia</i>	345	p.sph. (49 × 44 μ)	<i>T. strictus</i>	445	(545, 645 or 745) sph. (65 μ)

	NPC	Shape & size		NPC	Shape & size
Rhytiglosseae			<i>J. gendarussa</i>	345	p. (36 × 23 μ)
<i>Kalbreyerella rostel-</i>			<i>J. hyssopifolia</i>	244 ↑	(63 × 52 × 35 μ)
<i>lata</i>	244	sph. (77 μ)	<i>J. laevilinguis</i>	244 ↑	(49 × 37 × 28 μ)
<i>Fittonia verschaft-</i>			<i>J. matammensis</i>	244 ↑	(22 × 16 × 12 μ)
<i>feltii</i>	344	sph. (34 μ)	<i>J. natalensis</i>	345	p. (50 × 34 μ)
<i>Poikilacanthus gil-</i>			<i>J. platycarpa</i>	244 ↑	(51 × 35 × 26 μ)
<i>liesii</i>	744	p. (61 × 45 μ)	<i>J. procumbens</i>	244 ↑	(32 × 22 × ? μ)
<i>Rhacodiscus calyci-</i>			<i>J. ventricosa</i>	345	p. (55 × 35 μ)
<i>nus</i>	244 ↑	(65 × 36 × ? μ)	<i>Duvernoya adhatod-</i>		
<i>Rhytiglossa lactea</i>	244 ↑	(40 × 40 × 22 μ)	<i>doides</i>	244 ↑	(65 × 43 × ? μ)
<i>Brachystephanus</i>			<i>Adhatoda schimpe-</i>		
<i>africanus</i>	344 (444)	sph. (56 μ)	<i>riana</i>	244 ↑	(70 × 45 × 42 μ)
<i>Habracanthus syl-</i>			<i>A. vasica</i>	244 ↑	(60 × 42 × 36 μ)
<i>vaticus</i>	244 ↑	(37 × 37 × 25 μ)			
<i>Glockeria gracilis</i>	244	sph. (45 μ)	Pedaliaceae		
Justicieae			<i>Pedaliium murex</i>	643	o. (55 × 90 μ)
<i>Chaetothylax um-</i>			<i>Pterodiscus angu-</i>	543 (643, 743)	
<i>brosus</i>	244 ↑	(49 × 39 × 22 μ)	<i>stifolius</i>		o. (47 × 67 μ)
<i>Dianthera ciliata</i>	244 ↑	(64 × 40 × 32 μ)	<i>Harpagophytum</i>		
<i>D. collina</i>	244	sph. (50 μ)	<i>procumbens</i>	743	sp. (67 × 55 μ)
<i>D. comata</i>	345	sp. (28 × 22 μ)	<i>Holubia saccata</i>	543 (643, 743)	
<i>Jacobinia aurea</i>	244 ↑	(77 × 53 × ? μ)			sph. (70 μ)
<i>J. carnea</i>	244 ↑	(82 × 50 × ? μ)	<i>Uncarina aff. di-</i>		
<i>J. chrysostephana</i>	344	p. (68 × 46 μ)	<i>dieri</i>	543	p.sph. (67 × 59 μ)
<i>J. coccinea</i>	344 (444)	p. (60 × 38 μ)	<i>Rogersia adeno-</i>		
<i>J. pauciflora</i>	244 ↑	(70 × 43 × 32 μ)	<i>phylla</i>	743	p.sph. (67 × 59 μ)
<i>J. tenuistachys</i>	244 ↑	(38 × 26 × 20 μ)	<i>Sesamum angusti-</i>	743	p.sph.-sp. (57 ×
<i>Beloperone cali-</i>			<i>folium</i>		50 μ)
<i>fornica</i>	244 ↑	(75 × 50 × 40 μ)	<i>S. capense</i>	643	sp. (75 × 62 μ)
<i>B. plumbaginifolia</i>	244 ↑	(74 × 45 × 35 μ)	<i>S. indicum</i>	743	o. (41 × 60 μ)
<i>B. ramulosa</i>	244 ↑	(61 × 46 × 40 μ)	<i>Ceratotheca triloba</i>	743	sp. (62 × 50 μ)
<i>B. scorpioides</i>	244 ↑	(70 × 40 × 37 μ)	<i>Linariopsis pro-</i>		
<i>Dasytropis fragilis</i>	445	sp.-p. (50 × 36 μ)	<i>strata</i>	743 (745)	sp. (52 × 61 μ)
<i>Dejerella guttata</i>	344	p. (67 × 42 μ)	<i>Pretrea zangueba-</i>		
<i>Justicia adhatoda</i>	244 ↑	(66 × 47 × 40 μ)	<i>rica</i>	743	o.sph. (54 × 57 μ)
<i>J. championi</i>	244 ↑	(40 × 30 × ? μ)	<i>Josephinia afri-</i>		
<i>J. debilis</i>	244 ↑	(50 × 32 × 27 μ)	<i>cana</i>	743	sp. (41 × 47 μ)
<i>J. divaricata</i>	244 ↑	(40 × 26 × 16 μ)	<i>Niedzwedzkia semi-</i>	643 (743)	
			<i>retschenskia</i>		p.sph. (49 × 43 μ)

The exine patterns in the Acanthaceae are likewise very varied. From the psilate grains of *Habracanthus sylvaticus* to the complicated suprategillate reticulate grains of *Hypoestes antennifer* (Pl. 15, Figs. 1-4) is a wide range within which many grains with many different patterns are found.

In *Pseudocalyx africanus* (Pl. 23, Fig. 4) and *P. saccatus* the tegillum seems to be formed by the amalgamation of the part of the bacula which lies immediately below the capita.

Dicliptera assurgens, *D. scutellata*, *Jacobinia chrysostephana*, etc., are punctitegillate. A partial punctitegillate condition is encountered in *Duvernoya adhatodoides*, *Adhatoda schimperiana*, *Justicia divaricata* and *Thamnojusticia* sp. where the tegillum is restricted to the peripheral zone of the grain only.

The majority of the pollen grains show some form of reticulation, very big in *Barleria courtallica* (Pl. 39, Fig. 2), *Ruellia tessmanii* (Pl. 41, Fig. 2), etc. and very small in *Aphelandra lyrata* (Pl. 39, Fig. 1), *Chalarothyrsus amplexicaulis*, *Graptophyllum pictum*, etc. Reticula with simplibaculate muri are often homobrochate with a single pilum in each lumen, as in *Acanthus arboreus* and *A. longifolius*, or with many pila in each lumen as in *A. ilicifolius* (Pl. 3, Fig. 2), *Andrographis echiodoides* (Pl. 4, Figs. 1-3), *Anisacanthus abditus*, *Lophostachys falcata* (Pl. 18, Figs. 1-4) and *Asteracantha longifolia* or with a central, pointed pilum surrounded by many small, blunt pila as in *Crabbea acaulis* and *C. hirsuta*.

A fragmentimurate pattern is seen in *Aphelandra pulcherrima* and *Polytrema vulgare*.

Partially solid muri are seen in *Aphelandra lutea*, totally solid in *Phlogacanthus pubinervius*.

In *Brillantaisia lamium* and *Hypoestes antennifera* the tegillum is traversed by oblique puncta (Pl. 42, Fig. 2).

The "trema area" in the following plants is provided with insulae showing a reticulate pattern. These can be arranged in many different ways. In *Drejerella guttata* and *Beloperone californica* (Pl. 6, Fig. 6) there is a single row of more or less circular insulae on either side of the apertures. In *Beloperone plumbaginifolia* and *B. ramulosa* the insulae are in two rows, in *Dianthera ciliata* the insulae are in four rows, in *Chaetothylax umbrosus* they are scattered.

In *Ruellia*, the bacula are branched at the apex (cf. "columellae digitatae", Faegri and Iversen 1950). The branches seem to fuse to form the tegillum. In *Ruellia acutangula* the apex of the bacula branches into two, in *Ruellia angustiflora* it is still more branched (four or five branches). In *Ruellia neesiana*, *R. nitens* and *R. pacifica*, the apex of the bacula is much branched and the tegillar part of the muri traversed by narrow tubuli. In *Rhytiglossa lactea*

(Pl. 16, Fig. 3) and *Jacobinia carnea* (Pl. 16, Figs. 4–8) the apex of the bacula is likewise much branched. In *Bravaisia floribunda* (Pl. 32, Fig. 4), *B. tubiflora* and *Sanchezia klugii* (Pl. 35, Fig. 1) the base of the bacula is often hollow. In *Ruellia tessmannii* (Pl. 41, Fig. 2) and *Jacobinia carnea* (Pl. 33, Fig. 1) the bacula have small hollows both at apex and base.

SPORODERM STRATIFICATION

The study of "sporoderm stratification" (Erdtman 1952, p. 18) dates back to the year 1761. It was Koelreuter who used such terms as "hartes und weisses Häutchen" to describe the different layers.

However, credit also goes to the pioneering work of Fritzsche (1837) who established the terms exine and intine. He recognized four layers, intine, exintine, intexine and exine in the sporoderm. In the absence of a precise definition, his exintine and intexine are difficult to conceive.

Strasburger (1882) also used latinized terms, like intinium and exinium, and speaking about their development says: "Exinium die erste als ganzes zusammenhängende Haut der Sporen und Pollenkörner, intinium die zweite innere Haut, die von der ersten getrennt ist."

Fischer (1890) commenting on the above definition says: "Diese Art der Bezeichnungen würde zu den bedenklichsten Verwicklungen führen; denn nach Strasburger müsste man bei jeder Pflanzen-Spezies erst den gesamten Gang der Entwicklung kennen, um angeben zu können, was am fertigen Pollenkorn Exine, was Intine ist; eine Membran, der sich keine zweite hinzugesellt, wie es ja bei einigen Pflanzen vorkommt, müsste als Exine angesprochen werden, wiewohl sie in sämtlichen derartigen Fällen alle Merkmale einer Intine besitzt", and considers exine and intine as purely morphological terms having no connection whatsoever with their development and thus disagrees with Strasburger.

Potonié (1934) has contributed much towards the terminology of the sporoderm by giving a more exact definition to the above terms. He divides the sporoderm into an outer layer, the Exolamelle (syn. ectosexine), followed by an isolating or baculate layer, the Isolierschicht (syn. endosexine), a homogeneous layer, the intexine (syn. nexine) and an inner transparent layer, the intine.

The majority of the pollen grains have two layers, an outer resistant layer, the exine, and an inner non-resistant layer, the

intine. The subdivision of the exine (sensu lat.) as proposed by Fritzsche (1837) into exine (sensu str.) and intexine is confusing. To avoid this, some authors have used the term exoexine for Fritzsche's exine sensu str. In cases where the exine shows more than two layers Erdtman (1943) proposed the terms ekstexine (Fritzsche's exine sensu str.; exoexine) and endexine (for intexine) and in a general way described the "filling" between the two layers, as seen at the apertures of *Tilia americana*, as mesexine.

In 1948, he further proposed the division of the sporoderm into an outer sculptural layer, the sexine, a middle non-sculptural layer, the nexine, and an inner transparent layer, the intine. He divided the sexine into ecto- and endosexine, the nexine into ecto-, "meso"-, and endonexine.

However, Erdtman (1952) proposed a modification to his terminology, which, due to its clarity and brevity, has since been in vogue. He broadly sub-divides the sporoderm into an outer sculptural layer, the sexine, a middle non-sculptural layer, the nexine, and an inner transparent layer, the intine. The sexine can further be subdivided into ecto- and endosexine, the nexine into ecto- and endonexine.

Kuprianova (1956) in *Echinops sphaerocephalus* and Faegri (1956 a, b) in *Centaurea cyanus* distinguished two non-sculptural layers in the ectonexine. The outer layer of the nexine, which had the same staining properties as the sexine, was included in the sexine by Kuprianova. Faegri also included it in the sexine and named it the "footlayer".

Tomšovic (1960) calls this layer the "basosexine".

Morphologically speaking, the foot-layer is non-sculptural. It has been rightly referred to as the outermost layer of the nexine by Stix (1960) and named "nexine 1". She divides the ectonexine into an outer deep-stained nexine 1 and an inner light-stained nexine 2. Nexine 3 (endonexine) has not been found in the Compositae. However, Afzelius (1956) distinguishes two nexinous layers, ecto- and endonexine in *Carduus acanthoides*.

Nexine 3 or endonexine (syn. endexine, Kuprianova; mesine, Rowley) is the layer overlying the intine and is, as originally described by Erdtman (1952), "the inner more or less thin, more refractive zone of the nexine". Its thickness, presence or absence depends largely on fixation, chemical treatment, etc.

Afzelius (1955) showed in *Clivia miniata* that such a morpho-

logically distinct layer existed between the exine and intine as an electron dense lamellated layer.

Ehrlich (1958) also pointed out the presence of a thin endonexine in *Saintpaulia ionantha* which thickens under the apertures to form a lens-shaped body.

Rowley (1959), having found this layer in several dicotyledonous genera, used the term mesine (syn. endonexine, Erdtman; endexina, Kuprianova; nexine 3, Erdtman) and pointed out that this layer has the characteristics of both the underlying intine and the overlying exine and defined it as an intermediate, lamellated, electron dense layer. In the Commelinaceae this layer was termed endexine, as it was not lamellated, although electron dense.

In recent times, due to the advanced techniques, the study of the sporoderm has revealed details which may call for a revision of previously held conceptions and definitions. For instance, the nexine often shows some form of structure, either fine (as revealed by electron microscopy, cf. e.g. Afzelius 1956 etc.; cf. also Pl. 34, Fig. 4) or more coarse (cf. Fig. 2 a, p. 181 in Erdtman and Pragłowski 1959).

The species investigated, representing subfamilies and tribes of the Acanthaceae, have been sectioned from both fresh and herbarium material, according to the method described, and stained with basic fuchsin. The staining properties and the varying degree of absorption of the stain by the different layers have helped in the interpretation of the sporoderm stratification. Generally the sexine takes a deeper stain than the nexine and can thus be easily distinguished. The nexine has been found to be made up of two or three layers, viz. nexine 1 (syn. footlayer, Faegri; basosexine, Tomšovic), nexine 2 (syn. ectonexine, footlayer excluded) and nexine 3 (syn. endonexine).

Nexine 1 always takes a deeper stain than nexine 2 and nexine 3. This feature is especially prominent in sections made from acetolyzed grains. Acetolysis not only brings about a change in the chemistry of the sporoderm but also alters the index of refraction (Stix 1960) and furthermore destroys nexine 3 either completely or partially. Where partial destruction has taken place, this layer appears in places as streaks or small patches.

In sections made from fresh material the stain is more or less uniform; it is neither intensive nor does a sharp differentiation exist between the different layers.

In all grains where nexine 1 has been found, it is, as a rule, thinner than nexine 2. It forms either a deep-stained, continuous layer or is broken and restricted to the base of the bacula only. The thickness of this layer has also been found to be proportionate to the length of the bacula, i.e. it is thicker under the long bacula and thinner under the short bacula, as in *Peristrophe bicalyculata* (Pl. 34, Fig. 5). It is also either absent in the colpoid streaks, as in *Asteracantha longifolia* (Pl. 31, Fig. 3) and *Hygrophila angustifolia* (Pl. 33, Fig. 4) or present, as in *Jacobinia carnea* (Pl. 33, Fig. 1). Its outer margin is, as a rule, smooth, except in *Asystasia coromandeliana* (Pl. 37, Fig. 1) and *Ecbolium oreadam*, etc. where it is uneven.

Nexine 2 always forms a light-stained, compact, homogeneous layer with a smooth inner margin, as in *Drejerella guttata* (Pl. 32; Fig. 1), etc. or is undulating with occasional deep incisions, as in *Asteracantha longifolia*, or is broken in places showing small gaps, as in *Ruellia formosa*.

Nexine 3 is either totally or partially destroyed by acetolysis. Where it has been partially destroyed, its traces can be seen in places as small streaks or patches, as in *Mendoncia costaricana* (Pl. 34, Fig. 3). In sections made from fresh material this layer, if present, remains intact and forms a very thin, homogeneous layer which sometimes separates in places from the rest of the nexine as a loop, as has been seen clearly in *Strobilanthes alatus* (Pl. 38, Fig. 7), or thin and granular (granules less densely spaced towards the apertures), as in *Blepharis molluginifolia* (Pl. 32, Fig. 3).

In *Andrographis paniculata* it is extremely thin or probably absent, except at the apertures where it is light-stained and thickens to form a lens-shaped body.

In *Sesamum indicum* and *S. latifolium* it exists as a light-stained, thin layer throughout which also thickens at the apertures to form a lens-shaped body.

In *Barleria prionitis* (Pl. 31, Fig. 4) and *Lepidagathis cristata* (Pl. 34, Fig. 2) it exists as a light-stained layer which slightly thickens into a bulge at the apertures.

Descriptions of sections (species in alphabetical order):

Adhatoda vasica Pl. 31, Fig. 1; cf. also p. 65.—Nexine homo-

geneous, clearly distinguished into a continuous, thin, deep-stained nexine 1 and a thick, light-stained nexine 2.

Intine forms a uniform, transparent layer.

Andrographis paniculata (cult. Hyderabad) Pl. 31, Fig. 2; cf. also *A. echiioides*, p. 45 and Pl. 4, Figs. 1-5.—Sexine reticulate; muri thin, undulating, simplibaculate. Lumina polygonal, provided with small bacula.

Nexine homogeneous, very thin and not easily distinguishable into nexine 1 and nexine 2. Nexine 3 present as a thick, lens-shaped body at the apertures, probably also present as an extremely thin layer throughout.

Intine, broken in places, forms a transparent layer.

Asteracantha longifolia Pl. 31, Fig. 3; cf. also p. 29.—Sexine tenuitegillate, undulating, supported by densely spaced, slender bacula and provided with a suprattegillar reticulum consisting of low, solid muroid ridges.

Nexine homogeneous, clearly distinguished into a deep-stained nexine 1 and a light-stained nexine 2. Nexine 1 is present under the baculate layer and absent in the colpoid streaks. Inner surface of nexine 2 undulating with occasional deep incisions.

Asystasia coromandeliana Pl. 37, Fig. 1; cf. also p. 47 and Pl. 5, Figs. 1-5.—Sexine reticulate; muri simplibaculate. Bacula gradually decreasing in size towards the pores.

Nexine homogeneous, clearly distinguished into a deep-stained nexine 1 and a light-stained nexine 2. The thickness of nexine 1 is proportionate to the length of the bacula (thicker at centre of mesocolpia and gradually thinner towards the pores), outer surface uneven. Nexine 1 absent in the colpoid streaks or probably present as an extremely thin layer. Colpoid streaks provided with very small processes which appear more or less granular.

A prominent, granular, sexinous colpus membrane present.

Intine forms a uniform, thin layer, except at the apertures where it is distinctly thickened.

Barleria cristata (cult. Kew) Pl. 37, Fig. 2.—Sexine reticulate; muri simplibaculate.

Nexine homogeneous, clearly distinguished into a deep-stained nexine 1 and a light-stained nexine 2. Nexine 3 light-stained, extremely thin.

Intine forms a continuous, transparent layer.

B. prionitis Pl. 31, Fig. 4.—Sexine reticulate; muri simplibaculate. Bacula shorter, almost granuloid, towards the apertures.

Nexine homogeneous, clearly distinguished into a deep-stained nexine 1 and a light-stained nexine 2. Both these layers are traversed in places by narrow tubuli. Nexine 3 exists as a light-stained layer which slightly thickens into a bulge at the apertures.

Intine, broken in places and with occasional clefts, forms a transparent layer.

Blepharis boerhaviaefolia Pl. 32, Fig. 2; cf. also p. 40 and Pl. 7, Figs. 5–8.—Sexine reticulate; muri simplibaculate. Bacula gradually decreasing in size towards the apertures.

Nexine homogeneous, slightly thickened at centre of mesocolpia, gradually thinner towards apertures, clearly distinguished into a deep-stained nexine 1 and a light-stained nexine 2. The thickness of nexine 1 is proportionate to the thickness of the endosexine.

Intine forms a thin, continuous, transparent layer.

B. molluginifolia Pl. 32, Fig. 3.—Sexine reticulate; muri simplibaculate. Bacula gradually decreasing in size towards apertures.

Nexine homogeneous, slightly thickened at centre of mesocolpia and clearly distinguished into a deep-stained nexine 1, a light-stained nexine 2 and a deep-stained, densely granular nexine 3. Nexine 1 is of uniform thickness and has a smooth outer surface. Nexine 3 is sparsely granular towards the apertures.

Intine forms a thin, continuous, transparent layer.

Bravaisia floribunda Pl. 32, Fig. 4; cf. also p. 28 and *B. tubiflora*.—Sexine reticulate; muri simplibaculate. Large bacula hollow.

Nexine distinguished into a thin, continuous, deep-stained nexine 1 and a thin, more or less transparent layer showing varied structure. This layer can be seen to consist of small bacula, granules or fine lamellae. However, the fine details of this layer cannot be definitely determined; probably there is some sort of lamellation. Nexine 2 is granular and forms the bulk of the nexine. The granules are of varied thickness and densely spaced so as to give the appearance of a compact, homogeneous layer. Nexine 3 forms a very thin layer; its inner surface is uneven.

Crossandra undulaefolia (cult. Hyderabad) Pl. 37, Fig. 3; cf. also p. 42.—Sexine reticulate; muri simplibaculate.

Nexine homogeneous, distinguished into a deep-stained nexine 1 and a light-stained nexine 2.

Intine forms a continuous, thin, transparent layer (probably made up of thin, densely spaced, rod-like elements).

Dicliptera suberecta (cf. also p. 56).—Sexine punctitegillate. Tegillum undulating and supported by densely spaced bacula.

Nexine homogeneous, distinguished into a deep-stained nexine 1 and a light-stained nexine 2. Nexine 1 present under the baculate layer and absent in the colpoid streaks. Its outer surface smooth.

Intine forms a thin, transparent layer.

Drejerella guttata (cult. Hyderabad) Pl. 32, Fig. 1.—Sexine punctitegillate. Tegillum supported by slender bacula.

Nexine homogeneous, distinguished into a deep-stained nexine 1 and a light-stained nexine 2.

Intine forms a continuous, transparent layer.

Ecbolium oreadam Pl. 37, Fig. 4; cf. also p. 56.—Sexine punctitegillate. Tegillum thin, undulating, supported by slender bacula. Bacula gradually shorter towards apertures.

Nexine homogeneous, distinguished into a deep-stained nexine 1 and a light-stained nexine 2. Outer surface of nexine 1 coarse, uneven. Nexine 3 appears in places as thin, dark-stained streaks. Nexine 1 absent from the colpoid streaks.

Intine forms a continuous, thin, transparent layer.

Graptophyllum pictum Pl. 33, Fig. 3; cf. also p. 49.—Sexine reticulate; muri simplibaculate. Bacula longer at centre of mesocolpia, gradually shorter towards the apertures.

Nexine homogeneous, clearly distinguished into a deep-stained nexine 1 and a light-stained nexine 2. Nexine 1 restricted to the baculate layer, absent in the colpoid streaks or existing as a very thin layer only.

Hygrophila angustifolia (cult. Hort. Berg.) Pl. 33, Fig. 4; cf. also p. 30.—Sexine tectate, tenuitegillate. Tegillum undulating, supported by densely spaced, slender bacula and provided with a suprattegillar reticulum consisting of low, mureoid ridges.

Nexine homogeneous, distinguished into a deep-stained nexine 1 and a light-stained nexine 2. Nexine 1 restricted to the baculate layer only, absent in the colpoid streaks.

Intine forms a continuous, thin, transparent layer.

Hypoestes verticillaris (cf. also p. 54).—Sexine tectate, punctitegillate. Tegillum undulating, supported by bacula.

Nexine homogeneous, distinguished into a deep-stained nexine 1 and a light-stained nexine 2. Probable presence of nexine 3.

Jacobinia carnea Pl. 33, Fig. 1; cf. also p. 61.—Sexine tectate. Tegillum undulating, supported by bacula branched at apex.

Nexine homogeneous, distinguished into a continuous, deep-

stained nexine 1 and a light-stained nexine 2. Outer surface of nexine 1 uneven.

Intine continuous, transparent, slightly thickened at apertures.

J. coccinea Pl. 33, Fig. 5; cf. also p. 61.—Sexine tectate. Tegillum thin, undulating, supported by bacula. Bacula gradually shorter towards apertures, followed by a thin layer made up of thin, vertical, rod-like elements.

Nexine homogeneous, distinguished into a prominent, deep-stained nexine 1 and a light-stained nexine 2. Nexine 1 present in the colpoid streaks, its outer surface smooth.

Intine thin, continuous, slightly thickened at apertures.

Justicia betonica (cult. Hyderabad) Pl. 34, Fig. 1.—Sexine tectate, undulating, supported by bacula. Bacula gradually shorter towards apertures.

Nexine homogeneous, distinguished into a deep-stained nexine 1 and a light-stained nexine 2.

Intine thin, continuous, transparent, slightly thickened at apertures.

J. gendarussa (cult. Hyderabad) Pl. 37, Fig. 5; cf. also p. 63.—Sexine tectate, undulating, supported by bacula. Bacula gradually shorter towards apertures.

Nexine homogeneous, distinguished into a deep-stained nexine 1 and a light-stained nexine 2.

Intine thin, continuous, transparent, slightly thickened at apertures.

J. platycarpa Pl. 37, Fig. 6.—Sexine tectate. Tegillum undulating, supported by bacula. Bacula gradually shorter towards apertures.

Nexine homogeneous, distinguished into a deep-stained nexine 1 and a light-stained nexine 2. The thickness of nexine 1 is fairly proportionate to the length of the bacula.

Intine thin, continuous, transparent, slightly thickened at apertures.

Lepidagathis cristata (cult. Hyderabad) Pl. 34, Fig. 2.—Sexine reticulate; muri simplibaculate.

Nexine homogeneous, distinguished into a deep-stained nexine 1, a light-stained nexine 2 and a very thin, light-stained nexine 3 which slightly thickens into a bulge at the apertures.

Intine thin, transparent, broken in places.

Mendoncia costaricana Pl. 34, Fig. 3; cf. also *M. aspera*, p. 24

and Pl. 20, Figs. 4-7.—Total thickness of exine about 10 μ . Sexine punctitegillate. Tegillum slightly undulating, its outer surface coarse and uneven, supported by a thin, baculate layer.

Nexine 1 is absent. Nexine 2 evenly stained throughout, probably consisting of vertically arranged, very fine streaks. Nexine 3 appears in places as small patches.

Meyenia hawtayneana Pl. 34, Fig. 4; cf. also p. 25 and Pl. 21, Figs. 1-4.—Sexine tectate. Tegillum coarse and appears to be formed by densely spaced granules, followed by an infrategillar, granular layer. In this layer the granules are more densely spaced towards the upper surface, less densely towards the lower. It is supported by a thin layer made up of granules arranged in vertical streaks.

Nexine 1 absent. Nexine 2 consists of a thin, densely granular layer. Nexine 3 appears in places as small patches.

Peristrophe bicalyculata (cult. Hyderabad) Pl. 34, Fig. 5.—Sexine punctitegillate. Tegillum undulating, supported by densely spaced bacula.

Nexine homogeneous, distinguished into a deep-stained nexine 1 and a light-stained nexine 2. The thickness of nexine 1 is fairly proportionate to the length of the bacula. Colpus membrane sexinous, thin, granular.

Intine forms a prominent, continuous, transparent layer, slightly thicker towards apertures.

Phlogacanthus curviflorus Pl. 34, Fig. 6; cf. also p. 44 and Pl. 40, Fig. 3.—Sexine reticulate; muri simplibaculate. Bacula longer at centre of mesocolpia, gradually shorter towards the apertures.

Nexine homogeneous, distinguished into a deep-stained nexine 1 and a light-stained nexine 2. Outer surface of nexine 1 slightly uneven; inner surface of nexine 2 coarse, more or less granular (it probably represents an isolated nexine 3). Margin of apertures beset with small piloid processes.

Pseuderanthemum carruthersii (cult. Hyderabad) Pl. 33, Fig. 2.—Sexine reticulate; muri simplibaculate.

Nexine homogeneous, distinguished into a continuous, deep-stained nexine 1 and a light-stained nexine 2. Outer surface of nexine 1 coarse, uneven. In places nexine 2 appears as if made up of densely spaced, rod-like elements. Probable presence of nexine 3.

Intine forms a continuous, thin, transparent layer.

In the genus *Ruellia* the sexine is clearly distinguished into a distinct, reticulate pattern. Muri either simpli- or duplibaculate. Bacula of various shapes, showing different transitory stages of amalgamation.

The nexine in *Ruellia*, unlike the other acanthaceous genera described, is very compact and homogeneous and it is often very difficult to distinguish the different sublayers without staining. The following species have been sectioned: *Ruellia formosa*, *R. neesiana*, *R. patula*, *R. speciosa* and *R. tessmannii*.

Ruellia formosa Pl. 38, Fig. 1.—Sexine reticulate; muri duplibaculate.

Nexine homogeneous, distinguished into a dark-stained nexine 1 and a light-stained nexine 2 which is broken in places. Nexine 3 appears as thin, dark-stained streaks in places.

Intine forms an extremely thin, continuous, transparent layer.

R. neesiana.—Sexine reticulate; muri simplibaculate.

Nexine homogeneous, thin, not easily distinguishable into nexine 1 and nexine 2.

R. patula.—Sexine reticulate; muri simpli- and duplibaculate.

Nexine homogeneous, thin, not easily distinguishable into nexine 1 and nexine 2.

R. speciosa (cult. Hyderabad) Pl. 38, Fig. 2.—Sexine reticulate; muri simplibaculate. Bacula with hollows.

Nexine homogeneous, distinguished into a thin, dark-stained nexine 1 and a light-stained nexine 2.

Intine forms a thin, continuous, transparent layer.

R. tessmannii Pl. 38, Fig. 3; cf. also p. 38 and Pl. 41, Fig. 2.—Sexine reticulate; muri simplibaculate. Bacula branched, provided with hollows at apex and base.

Nexine homogeneous, distinguished into a deep-stained nexine 1 and a light-stained nexine 2 and nexine 3. Inner surface of nexine 3 uneven in places and granular.

Sanchezia klugii Pl. 35, Fig. 1; cf. also p. 27 and Pl. 28, Figs. 1-4; cf. also *Bravaisia floribunda* Pl. 32, Fig. 4.—Sexine reticulate; muri simplibaculate. Bacula hollow at base.

Nexine homogeneous, distinguished into a deep-stained nexine 1 and a light-stained nexine 2. Probable presence of a thin nexine 3. Nexine 1 restricted to the base of the bacula.

Spathacanthus hoffmanni Pl. 38, Fig. 5; cf. also p. 46.—Sexine tectate. Tegillum thick, undulating, supported by densely spaced bacula.

Nexine homogeneous, thinner at centre of mesocolpia, thicker towards apertures, distinguished into a thin, deep-stained nexine 1 and a light-stained nexine 2. Outer surface of nexine 1 uneven. Probable presence of a thin nexine 3.

Stenandrium dulce (cult. Hyderabad) Pl. 38, Fig. 6.—Sexine tectate. Tegillum undulating, supported by slender bacula. Bacula gradually shorter towards apertures.

Nexine homogeneous, distinguished into a deep-stained nexine 1 and a light-stained nexine 2.

Intine thin, continuous, slightly thicker at the apertures.

Strobilanthes alatus Pl. 38, Fig. 7; cf. also p. 33 and Pl. 29, Figs. 12–14.—Sexine reticulate; muri simplibaculate.

Nexine homogeneous, distinguished into a deep-stained nexine 1, a light-stained nexine 2 and a deep-stained nexine 3. Outer surface of nexine 1 uneven. It has been observed that in places the thin, uneven nexine 3 separates from the rest of the nexine in the form of a loop.

Thunbergia fragrans (cult. Hyderabad) Pl. 35, Fig. 3; cf. also p. 26 and Pl. 30, Figs. 8–10.—Sexine tectate. Tegillum deep-stained, rough, uneven and densely granular, supported by a light-stained layer made up of slender, rod-like elements. The latter are granular in composition.

Nexine dark-stained, densely granular, not differentiated into nexine 1 and nexine 2.

Intine forms a thick, continuous, transparent layer.

The sexine is provided with long, blunt processes, quite unlike the suprattegillar processes met with in the Acanthaceae and other families. The body of the processes appears to be the thickened part of the nexine which also protrudes into the lumen of the grain thereby causing a depression in the underlying intine. The outer main part of the processes is covered by the tegillum and rod-like elements. The basal part is more solid than the apical. The apical part appears loose and spongy; the interior elements are probably ramified. Aperture covered by deep-stained, granular, sexinous elements.

T. grandiflora (cult. Hyderabad) Pl. 36, Figs. 1, 2.—Sexine tectate. Tegillum deep-stained, rough and appears to be made up of densely spaced granules, supported by a light-stained, thick, less densely spaced, granular layer.

Nexine dark-stained, densely granular, not differentiated into nexine 1 and nexine 2.

Intine forms a thick, continuous, transparent layer, probably lamellated.

Sesamum indicum Pl. 35, Fig. 2 and *S. latifolium* (cult. Hyderabad) Pl. 38, Fig. 4.—Sexine made up of short, piloid processes, granular in composition, followed by a thick, granular layer. The granules in the latter are evenly spaced, except at the base of the layer where they are arranged in short, vertical streaks.

Nexine consists of a thin, uneven, densely spaced, granular layer. Nexine 1 absent. Nexine 3 forms a light-stained, thin layer which thickens into a lens-shaped body at the apertures.

The fact that sporoderm stratification can act as a reliable guide in taxonomy cannot be denied. Apertures, shape, size, etc. are also important, although these characters vary sometimes to a very great extent (Maurizio 1956 and others).

The exact mode of development of the sporoderm, from the 'primitive' to the 'advanced', is still very difficult to determine. But in relation to the gross morphology of the plant, the different layers of a sporoderm, the presence or absence of one layer or the other, its composition, etc. can point at the fact that the species, the tribe, or the family is either 'primitive' or 'advanced'.

Thus in the highly evolved family Compositae, the detailed study of the complicated sporoderm stratification by Stix (1960) has revealed that the nexine is distinguished into a well developed nexine 1 (about $1-2\ \mu$ thick) and a nexine 2. In the Vernoniaceae (e.g. *Vernonia scorpioides*, l.c., Pl. 2, Fig. 2), the nexine 1 is thin. In the Cynareae and Mutisieae (cf. *Carlina acaulis*, Pl. 5 A, *Centaurea cyanus*, Fig. 35, p. 88, *Echinops banaticus*, Pl. 8, and *Mutisia viciaefolia*, Pl. 2) nexine 1 is very thick. Taxonomically the former species is considered "primitive", the latter "advanced". The probable absence of nexine 3 is yet another feature in this highly evolved family. The presence of nexine 3, considering the degree of thickness of this layer, would mean that the species is not 'advanced' but 'primitive'.

In view of the findings of Stix (1960), the "ecto- and endonexine" shown in Afzelius's (1956) electron micrograph of *Carduus acanthoides* can be interpreted as nexine 1 and nexine 2. Thus the presence of nexine 1 or nexine 3, their relative thickness etc. may indicate that a species, a tribe or a family be 'primitive' or 'advanced'.

This feature is well pronounced in the Acanthaceae where the sporoderm shows varied stratification. The sexine is either simple, as in the Thunbergioideae, or well differentiated, as in the Acanthoideae, Nelsonioideae and Mendoncioideae. As regards the nexine, it has been observed that in some species, besides nexine 2, both nexine 1 and nexine 3 are present. In other species either nexine 1 or nexine 3 is absent. In a few species the nexine forms a homogeneous layer without differentiation into nexine 1, 2 and 3.

Out of the four subfamilies recognized by Lindau, viz. Nelsonioideae, Mendoncioideae, Thunbergioideae and Acanthoideae, the sporoderm stratification in the last three subfamilies has been investigated by sectioning. The material of Nelsonioideae was not sufficient for sectioning. However, my study of the sporoderm stratification of this subfamily is based on a careful microscopical examination of the optical section.

In the Nelsonioideae the sporoderm is distinctly differentiated into sexine and nexine. The sexine is well developed and consists of ecto- and endosexine. The nexine forms a distinct, homogeneous layer without any differentiation into nexine 1 and nexine 3.

In the Mendoncioideae (cf. *Mendoncia costaricana* Pl. 34, Fig. 3) the sporoderm is the thickest encountered in the Acanthaceae. It is distinguished into a thin sexine and a thick nexine. The sexine is further distinguished into an ecto- and an endosexine, both granular in composition. The nexine is the thickest met with in the Acanthaceae. Nexine 1 is absent. Nexine 2 consists of a thick, granular layer (granules either evenly spaced or forming vertical, rod-like elements in places). Nexine 3 appears in patches and is also granular in composition. This isolated nature of nexine 3 is due to its being partially destroyed by acetolysis. The granular nature of the sexine, the absence of nexine 1 and the presence of nexine 3 all point towards the 'primitive' nature of the subfamily Mendoncioideae.

In the Thunbergioideae the sporoderm is as thick as in the Mendoncioideae and consists of a thick, granular sexine and a thin, granular nexine. The sexine is, as a rule, not developed into ecto- and endosexine. As to the concentration of the granules, the outer layer of the sexine in *Thunbergia* (Pl. 35, Fig. 3 and Pl. 36, Figs. 1, 2) and *Meyenia* (Pl. 34, Fig. 4) can be interpreted as a tegillum, supported by a thick, granular layer. In *Pseudocalyx* (Pl. 23, Fig. 4) the granules are arranged to form thin, densely spaced, vertical streaks which partially fuse to form a tegillum.

Nexine 1 is absent in the Thunbergioideae. Nexine 2 consists of a thin layer, densely granular. Nexine 3 is absent (except in *Meyenia*). The intine is thick, transparent, probably lamellated. Sporoderms with granular sexine and nexine consisting of thin, granular layer without differentiation into nexine 1 and nexine 3 (except in *Meyenia* where nexine 3 is found in places), may be considered simple, perhaps even more 'primitive' than the sporoderm type encountered in the Mendoncioideae.

Out of the four genera included under the Thunbergioideae, the genus *Thunbergia* appears to be the less 'advanced', since its sporoderm corresponds exactly to the one described above. The genus *Pseudocalyx* is slightly more 'advanced' than *Thunbergia*, as its sporoderm shows a clearer differentiation into sexine and nexine and furthermore, the sexine appears developed, as it consists of slender, piloid processes. The sporoderm stratification of *Meyenia*, differs very much from that of the above genera because of the arrangement of the granules. These are not evenly spaced and further, they are arranged in the form of short, slender, vertical rods towards the nexine, thereby appearing as a thin, baculate layer. Nexine consists of a thin, granular layer. Nexine 1 is absent but nexine 3 (partially destroyed by acetolysis?) is, as mentioned above, present in places. The above characteristics of the sporoderm are quite unlike those met with in the Thunbergioideae but are strikingly similar to the sporoderm stratification in the Pedaliaceae, especially that of *Sesamum latifolium* (Pl. 38, Fig. 4).

The genus *Pounguia* (Pl. 22, Fig. 6) has a well developed sporoderm. The sexine is tectate and appears to be formed by the amalgamation of densely spaced, slender bacula. Nexine 1 is absent. Nexine 2 forms a thick, homogeneous layer. Nexine 3 is present; in places it thickens or forms outgrowths.

In the genera of the different tribes of the subfamily Acanthoideae sexine and nexine are distinctly differentiated. Further, the nexine shows a differentiation into nexine 1, nexine 2 and nexine 3. Nexine 1 has been traced in all except Louteridiaceae, Haselhoffiaceae, Rhombochlamydeae, Pseuderanthemeae and Isoglosseae, the pollen grains of which could not be sectioned due to insufficient material. But on the basis of careful microscopical studies of the optical sections, the presence of nexine 1 and the absence of nexine 3 in the above tribes is assumed.

In the tribes Strobilantheae, Barlerieae and Andrographideae, the

exine in *Strobilanthes alatus* (Pl. 38, Fig. 7), *Barleria prionitis* (Pl. 31, Fig. 4), *B. cristata* (Pl. 37, Fig. 2), *Lepidagathis cristata* (Pl. 34, Fig. 2) and *Andrographis paniculata* (Pl. 31, Fig. 2) shows, besides nexine 1, a nexine 3 which is slightly thickened at the apertures. In *Andrographis paniculata* the nexine forms a thin, homogeneous layer without a distinct differentiation into nexine 1 and nexine 2. Nexine 3 forms a very thin layer or is probably absent, except at the apertures where it thickens to form a lens-shaped body. (The same type of lens-shaped thickening of nexine 3 can be seen in the genus *Sesamum*.)

Thus the subfamily Acanthoideae is considered a more 'advanced' group of tribes than the other three subfamilies, due to the presence of nexine 1 and the absence of nexine 3. The different tribes and genera grouped under it can also be referred to as more 'advanced' or less 'advanced' on the basis of the characteristics of the sporoderm.

Out of the 18 tribes included under the subfamily Acanthoideae, the tribes Justicieae, Odontonemeae, Graptophylleae, Asystasiaceae, Aphelandreae, Acantheae, Ruellieae, Petalidieae, Hygrophileae and Trichanthereae, all have a well developed nexine 1 and, as nexine 3 is absent or faintly present, they may perhaps be more 'advanced' than the tribes Strobilantheae, Barlerieae and Andrographideae which have both a nexine 1 and nexine 3.

Similarly, the different stages of development of nexine 1, i.e. thick or thin, continuous or broken, does also point at the more 'advanced' or less 'advanced' condition of the species or tribe.

Thus Justicieae, Aphelandreae and Acantheae have all a well developed, continuous nexine 1 and are therefore more 'advanced' than Trichanthereae, Hygrophileae, Petalidieae, Ruellieae, Asystasiaceae and Odontonemeae, where nexine 1 does not form a continuous layer. In spite of having a continuous nexine 1, the tribes Strobilantheae, Barlerieae and Andrographideae also have a nexine 3 which points at their less 'advanced' stage.

Thus one may conclude that the granular nature of the sporoderm, viz. thick, granular sexine (without proper differentiation into ecto- and endosexine) and thin, granular nexine (without differentiation into nexine 1, 2 and 3), as met with in *Thunbergia*, etc., is a 'primitive' condition, whereas the sporoderm, as seen in *Justicia*, etc., with its well developed sexine (ecto- and endosexine) and nexine (nexine 1 and nexine 2 only), is an 'advanced' condition.

In conclusion it would perhaps be possible to consider that apertures met with in genera with a 'primitive' type of sporoderm (*Thunbergia* etc.) be more 'primitive' than those met with in genera with more 'advanced' type (*Justicia* etc.).

Thus the aperture development may perhaps proceed from a spirotrema, via a colpate and colporate to a porate status.

The above discussion gives an insight into the difficulties, tricky problems and obstinate perplexities one has to face in dealing with sporoderm stratification. In any case it tends to "show that pollen morphology is more complicated—and at the same time probably more useful in taxonomical and phylogenetic context—than has hitherto been realized" (Erdtman 1960 a).

Taxonomical suggestions

Lindau based his subfamily Nelsonioideae on the genus *Nelsonia*. His description of the pollen grains of *Nelsonia* as "typischer Spaltenpollen, Spalten sehr schmal, ohne Poren" (1893) and again "Spaltenpollen mit Poren" in the Pflanzenfamilien (1895) are contradictory.

Bhaduri (1944) doubted the validity of the subfamily Nelsonioideae and expressed an opinion that, as the pollen grains of *Nelsonia canescens* very much resemble the pollen grains of *Andrographis paniculata*, it ought to be shifted to the vicinity of the tribe Andrographideae. The above cannot be accepted, as the pollen grains of *Nelsonia canescens* do not resemble the pollen grains of *Andrographis paniculata*. The pollen grains of the former are 3-colpate, whereas those of the latter are 3-colporate (cf. also *Andrographis echinoides*, Pl. 4, Figs. 1–5, and p. 45) with colpi with thick margins and equatorial constriction, etc.

Recently Johri and Hardev Singh (1959), dealing with the morphology, embryology and systematic position of *Elytraria acaulis*, came to the conclusion that *Elytraria* be retained in the subfamily Nelsonioideae of the family Acanthaceae. The arguments brought forward by them for returning the Nelsonioideae to the Acanthaceae are not convincing and partly incorrect, as, e.g., the statement regarding the presence of retinacula (jaculators) in *Elytraria*. That the seeds of *Andrographis* would be round, is also a mistake. They are not so strongly flattened as most of the seeds of the other genera, but they are certainly not globose like those of the Nel-

sonioideae. The description and figure of the structure of the capsule, given by the above authors, are not correct either, for the dissepiment is in reality complete, although it easily splits into two when a section is cut, and the parts they regard as placenta are in reality the swollen funicles (there is, of course, a difference between a swollen funicle and a funicle that has grown out into a retinaculum). Even the figure and description of the pollen grain of *Elytraria acaulis* as 3-colporate (syncolpate) are not correct because the pollen grains are distinctly 3-colpate. A syncolpate condition is not found in the Acanthaceae, except in *Blechum*. The sentence with which they conclude their paper, "However, they (i.e. the aberrant characters) do not warrant the transfer of *Elytraria* to the Scrophulariaceae, and for the present its inclusion in the family Acanthaceae . . . appears to be the most satisfactory course", is incomprehensible, because the authors do not mention any characters which would exclude it from the Scrophulariaceae. Furthermore, their contention that the characters by which the Nelsonioideae differ from the true Acanthaceae are of no sufficient importance to separate it from the latter, is not made clear by them.

Out of the genera included under the subfamily Mendoncioideae, *Mendoncia* (cf. *Mendoncia aspera*, Pl. 20, Figs. 4-7) and *Monachochlamys* have brevissimicolpate, prolate spheroidal pollen grains. Moreover, the exine is crassinexinous (cf. *Mendoncia costaricana*, Pl. 34, Fig. 3). Thus these genera with their typical apertures and sporoderm stratification seem to form a close-knit group. The inclusion of *Gilletiella* (cf. *Gilletiella congolana*, Pl. 12, Fig. 9) with its colpate pollen grains with relatively long colpi and thin nexine, does not seem to be correct. A better place for it would perhaps be in the tribe Acantheae, in the vicinity of *Blepharis*.

With the exclusion of *Gilletiella*, the subfamily Mendoncioideae would consist of two genera only which, on account of pollen morphology, are distinctly different from the rest of the genera of the Acanthaceae. In spite of an affinity to the genera grouped under Thunbergioideae (cf. the presence at the base of the thecae of a curious, rounded appendage with a ring of conical bristles, as mentioned by Bremekamp 1955 e, p. 13), it seems quite justifiable to raise the Mendoncioideae to a family rank (Mendonciaceae).

With the inclusion of Benoist's genus *Pounguia* (cf. *Pounguia purpurata*, Pl. 22, Figs. 5, 6) the number of genera included under

Thunbergioideae has risen to four. Out of these, *Thunbergia* and *Pseudocalyx* resemble each other very much. The sporoderm stratification also points at their close affinity and at the same time at the perhaps more evolved condition of *Pseudocalyx*.

The pollen grains of *Poungia* are oblate. They are provided with two narrow, circular grooves, one in each face (sometimes they fuse to form a spiral). The exine shows a clear differentiation into sexine and nexine and both these layers appear well developed. From the above characters *Poungia* seems to be an evolved genus. The line of evolution seems, as already mentioned, to proceed from a spirotreme to a porate condition. The suggestion by Bremekamp (1955 e) that *Poungia* be excluded from the Thunbergioideae and included in the Whitfieldieae, a tribe of the Acantheae created by him (1944), does not seem to be justified. The Whitfieldieae is based on the genus *Whitfieldia* (cf. *Whitfieldia longifolia*, Pl. 30, Figs. 11–13) which has spheroidal, porate pollen grains much different from those in *Poungia*.

The monotypic genus *Meyenia* (cf. *Meyenia hawtayneana*, Pl. 31, Figs. 1–4 & Pl. 34, Fig. 4) happens to be a controversial genus in the subfamily Thunbergioideae. The aberrant characters of the pollen grains were first pointed out by Radlkofer. Bremekamp (1955 e) has pointed out the doubtful taxonomic position of the genus. The pollen grains with their oblate shape and very narrow colpi are strikingly similar to the pollen grains met with in the Pedaliaceae and strikingly dissimilar to the pollen grains of the genera grouped under Thunbergioideae. Moreover, the sporoderm stratification also closely resembles that of Pedaliaceae, especially that of *Sesamum latifolium* (Pl. 38, Fig. 4). Thus pollen morphology and gross morphology (the main difference being the more or less regularly 5-lobed calyx as against the many-toothed calyx; cf. Lindau 1895) are both in favour of excluding *Meyenia* from the subfamily Thunbergioideae and including it in the Pedaliaceae (in the vicinity of the genus *Sesamum*).

With the exclusion of *Meyenia*, the Thunbergioideae comprises closely related genera which are distinctly different from the rest of the acanthaceous genera and therefore deserves to be raised to a family rank (Thunbergiaceae).

Lindau's subfamily Acanthoideae has been subjected to many changes, especially by Bremekamp. The many changes proposed by him have already been listed in the introduction. The genera in-

vestigated are discussed below (according to Lindau's classification).

The genera grouped under Trichanthereae form a homogeneous group. Their 2-porate pollen grains, characteristic arrangement of the colpoid streaks, semicircular sexinous patches around the apertures and sporoderm stratification all point towards the homogeneity of the tribe.

Louteridieae, with the single genus *Louteridium* (cf. *Louteridium donnell-smithii*, Pl. 19, Figs. 1-3), forms a unique tribe. The large-sized pantoporate pollen grains and the presence of gemmae and verrucae distinguish it from the rest of the tribes in the Acanthaceae.

A somewhat similar type of pollen grains occur in *Stenandrium trinerve* (Pl. 29, Figs. 8-11) and *S. pohlii*, which, however, belong to an entirely different tribe, Aphelandreae. Due to the small size and anomotreme condition of the pollen grains, *Stenandrium* cannot be included under the Louteridieae.

Bremekamp's (1944) contention "I have found that the kind of pollen which was considered peculiar to the Louteridieae, occurs also in some of the Ruellieae, and as no other important differences between the two tribes appear to be present, it seems inadvisable to retain the Louteridieae as an independent tribe" is not proof enough to reduce it into a subtribe of the Ruellieae, as in the present investigation the Louteridieae-type of pollen grains has not been encountered elsewhere in the family. In the absence of more exact information as to genera with this type of pollen, it seems reasonable to retain it as an independent tribe.

The genera grouped under Hygrophileae, except *Mellera* (cf. *Mellera lobulata*, Pl. 20, Figs. 1-3), have a more or less uniform type of pollen grains. All have colpoid streaks. The grains in *Astercantha longifolia*, *Brillantaisia emini* (Pl. 9, Figs. 1-4), *B. lamium*, *Hygrophila costata* and *H. spinosa* are 4-colporate, and provided with a suprareticulate pattern, those in *Brillantaisia madagascariensis* 4-colporate with suprattegillar spinules, those in *Hygrophila ayatensis* and *H. pringlei* 3-colporate, tectate. The pollen grains of *Mellera*, with their colpoid streaks and semicircular sexinous patches around the apertures, resemble very much the pollen grains of Trichanthereae.

In the Petalidieae the pollen grains of *Blechum* (cf. *Blechum rownei*, Pl. 7, Figs. 1-4) are 3-colporate-syncolpate, a condition not

met with in the other genera of the family. Bremekamp's (1948) observation that the exine is "without any relief" is, as also shown by Erdtman (1952, Fig. 6, p. 31), not correct, as the sexine exhibits a distinct homobrochate reticulation. The grains are not similar to those of *Barleria* and *Lepidagathis*. As regards *Phayloopsis* (cf. *Phayloopsis longifolia*, Pl. 40, Fig. 1) and *Petalidium*, their pollen grains resemble those of *Mellera* (Hygrophileae) and also those of the genera included under the Trichanthereae.

In the Strobilantheae the pollen grains of *Aechmanthera*, *Calophanes*, *Dyschoriste*, *Mimulopsis*, *Stenosiphonium* and *Sympagis* (cf. *S. brunoniana*, Pl. 29, Figs. 12-14) are 3-colporate. Those in *Acanthopale* (Pl. 1, Figs. 1-4) are pantoporate and the exine is provided with blunt, spinoid processes. Bremekamp (1944) in his large monograph of the Strobilanthinae, a subtribe of the Ruellieae, has dealt with the taxonomy of this group in detail. The pollen grains of *Acanthopale*, however, are quite distinct from those of the rest of the genera.

The tribe Haselhoffieae is represented by a single genus, *Haselhoffia* (cf. *H. nematosiphon*, Pl. 40, Fig. 4). The 3-colpate condition, exine pattern, etc. suggest that it may be near to Acantheae and not, as regarded by Lindau, a close ally of the Strobilantheae. It may therefore be referred to the Acantheae.

The pollen grains of the tribe Ruellieae vary to a great extent. In *Forsythiopsis* (cf. *F. baroni*, Pl. 12, Figs. 1-4) they are colpate, those in *Eranthemum*, *Whitfieldia* (cf. *W. longifolia*, Pl. 30, Figs. 11-13) and *Ruellia* (cf. *R. tessmannii*, Pl. 41, Fig. 2) porate. The treatment of *Forsythiopsis* as congeneric with *Ruttia* (Odontomeae) seems correct according to pollen morphology.

The genera included under Barlerieae form a homogeneous group. The sexine pattern is uniformly reticulate (hetero- or homobrochate). However, there are differences with regard to the apertures. The pollen grains of *Barleria* and *Crabbea* are porate, those of *Lepidagathis*, *Lophostachys* and *Barleriola* are colpate. Nevertheless, the sporoderm stratification shows a close affinity between *Barleria* (cf. *Barleria prionitis*, Pl. 31, Fig. 4) and *Lepidagathis* (cf. *Lepidagathis cristata*, Pl. 34, Fig. 2). Both show nexine 1, which in *Barleria* is well developed. Nexine 3 forms a thickened layer at the apertures. In *Barleria* a few grains show an indication of a faint colpus. Taking the above into consideration, it may well be stated that *Barleria* and *Crabbea* are more

evolved than *Lepidagathis*, *Lophostachys* and *Barleriola* and that the porate condition has evolved from a colporate status. Further, the pollen grains of Barlerieae, in spite of a superficial resemblance to those of Ruellieae, especially *Barleria* and *Ruellia*, differ very much in their sporoderm stratification and the two tribes do not seem to show a close affinity, as presumed by some taxonomists.

The genera of the Acantheae form a homogeneous group. All are 3-colpate and show a more or less similar sexine pattern. Moreover, the genera closely resemble those of the Aphelandreae.

The genera grouped under Aphelandreae form a homogeneous group and resemble those of the Acantheae. Two species of *Stenandrium*, *S. trinerve* (Pl. 29, Figs. 8–11) and *S. pohlii* have, however, pollen grains with a superficial resemblance to the pollen grains of *Louteridium*.

The tribe Rhombochlamydeae consists of a single genus, *Rhombochlamys* (cf. *Rhombochlamys elata*, Pl. 25, Figs. 1–4), the pollen grains of which are 3-colpate. The colpi are broad with tapering ends. Furthermore they have an incrassate membrane and a marginal part which is densely and finely granular. Thus the pollen grains do not resemble those of the Aphelandreae. Regarding Rhombochlamydeae Lindau says "Äusserlich hat die Gattung mit *Aphelandra* Ähnlichkeit". He then placed it near the Andrographideae, as he regarded the pollen as "Daubenpollen", a type that was known so far from the Andrographideae only. In the Latin description of this genus he says that it resembles the pollen grains of *Asystasia*, which belongs to a different type altogether, known as "Rahmenpollen". At any rate the pollen grains of *Rhombochlamys* are quite distinct and cannot be compared to those of the Andrographideae or *Asystasia* due to the absence of pores, or to the Aphelandreae or Haselhoffieae due to the deviating nature of the apertures but ought to be retained as an independent tribe.

The genera investigated in the Andrographideae have pollen grains which are quite distinct due to the thickened colpi margins, lalongate ora, supracreticulate pattern, etc. and therefore form a well defined group.

The Asystasieae show various forms of pollen grains. *Asystasia* (cf. *Asystasia coromandeliana*, Pl. 5, Figs. 1–5) is, due to the 3-porate pollen grains, arrangement of colpoid streaks, etc., distinct from *Thomandersia* (cf. *Thomandersia laurifolia*, Pl. 30, Figs. 4–7), where the pollen grains are oblate, colpate and without colpoid

streaks, etc. The pollen grains of *Styasasia* (cf. *Styasasia* sp., Pl. 30, Figs. 1-3) are spheroidal, porate and spinulose. The genera *Spathacanthus*, *Chamaeranthemum*, *Hulemacanthus* (cf. *Hulemacanthus whitei*, Pl. 14, Figs. 1-4) and *Chalarothyrsus* have colporate pollen grains which closely resemble each other. The pollen grains of *Thomandersia* resemble those of *Meyenia* and are entirely different from those of the genera of the Acanthaceae. Pollen morphology is in favour of its being referred to the Pedaliaceae (cf. also Bremekamp 1942).

The tribe Graptophylleae constitutes a homogeneous group. The pollen grains of the genera investigated are either colporate or porate. The porate grains have wide colpoid streaks which give the appearance of a colporate condition. Besides, intermediate stages leading from a colporate to a porate status are often found. The sexine pattern is more or less the same in all genera.

The tribe Pseuderanthemeae and the genera investigated form a homogeneous group. The pollen grains are colporate and provided with a more or less uniform sexine pattern.

The Odontonemeae, the largest tribe of the Acanthoideae, have various types of pollen grains. The genus *Rungia* with its 2-porate pollen grains, sexine showing insulae, etc. does not fit in this tribe. A better place for it would be in the Justicieae (cf. also Bremekamp 1943).

The Rhytiglosseae do not form an entirely homogeneous group. The pollen grains are porate and the sexine is either reticulate, tectate or, as in *Poikilacanthus*, made up of polygonal insulae. In the tectate grains the tegillum is provided with either spines, spinules or verrucae. However, the shape of the pollen grains and the number of apertures, etc. do not suggest any affinity to the Trichanthereae. Bremekamp's (1938) contention that, "the genus *Rhacodiscus* which, on account of its pollen characters, was separated by Lindau from *Justicia* and put in the Isoglosseae Porphyrocominae, is returned here to its former position" does not seem to be justified. Lindau no doubt was right in separating *Rhacodiscus* from *Justicia* on account of the pollen characters. The pollen grains of the above two genera, although 2-porate, are, due to the presence of verrucae in *Rhacodiscus* (cf. *Rhacodiscus calycinus*, Pl. 24, Figs. 1-4), sufficiently distinct to be separated. The pollen grains of *Poikilacanthus* (cf. *Poikilacanthus gilliesii*, Pl. 22, Figs. 1-4) do not resemble those of the "Ruelliinae", as Bre- me-

kamp (1938) had assumed, for the sexine is not "alveolate" but made up of polygonal insulae, a condition not encountered in any other genera of the Acanthaceae. According to Lemée (1931) the genera *Glockeria* and *Habracanthus* are, on account of their flowers, very closely related. He even suggests the possibility of uniting the two genera. The pollen characters, however, do not support this suggestion.

The Justicieae, as far as investigated, seem to form a homogeneous group. All have porate pollen grains (in some species there is a faint indication of a colpus) and the sexine pattern is more or less the same.

Addendum:

Some of the photomicrographs of fossil pollen grains published by Kuyl, Muller and Waterbolk (1955) show a striking resemblance to some of the acanthaceous pollen grains described in the present paper.—Pl. 4, Fig. 2, from the Miocene, Nigeria, resembles *Ruellia* (cf. *R. angustiflora*, Pl. 25, Fig. 5).—Pl. 4, Fig. 6, from the Miocene, Nigeria, resembles *Hulemacanthus* (cf. *Hulemacanthus whitei*, Pl. 14, Figs. 1–4).—Pl. 5, Figs. 1, 8, 9, from the Tertiary, Trinidad, resembles the pollen grains of the genera *Steirosanchezia*, *Sanchezia* (cf. *Sanchezia klugii*, Pl. 28, Figs. 1–4) and *Bravaisia* of the tribe Trichanthereae.

Summary

A total of 260 species from 103 genera have been investigated. Diagnoses of 130 species from 98 genera have been provided (pp. 23–68).

Diagnoses of 14 species from 12 genera in the Pedaliaceae have also been given (pp. 65–68).

The smallest grains were found in *Staurogyne mandioccana* ($29 \times 24 \mu$), *Monothecium aristatum* ($25 \times 20 \mu$) and *Nelsonia canescens* ($25 \times 15 \mu$), the largest in *Barleria courtallica* ($127 \times 107 \mu$), *Louleridium donnell-smithii* (140μ) and *Thunbergia venosa* (105μ).

With regard to apertures, it has been observed that transitions met with point towards the possibility of a porate status having evolved from a colpate via a colporate status.

Hollow bacula are met with in *Asystasia*, *Bravaisia floribunda*, *B. tubiflora*, *Jacobinia carnea*, *Ruellia tessmannii* and *Sanchezia*.

Pollen grains of 38 species from 28 genera in the Acanthaceae and one genus in the Pedaliaceae have been sectioned and descriptions provided (pp. 80-88).

The nexine consists of two or three layers (except in *Thunbergia*).

Nexine 1 always takes a deeper stain than nexine 2 and nexine 3. This feature is especially prominent in sections made from acetolyzed grains. In sections made from fresh material the stain is more or less uniform; it is neither intensive nor does a sharp differentiation exist between the different layers.

In all pollen grains where nexine 1 has been found, it is, as a rule, thinner than nexine 2. It forms either a continuous layer or is broken and restricted to the base of the bacula only. The thickness of this layer has been found to be greater under the long bacula than under the short ones. In the colpoid streaks it is either present or absent.

Nexine 2 forms a light-stained, compact, homogeneous layer with a smooth inner margin. It is sometimes undulating with occasional deep incisions and may in places even be broken.

Nexine 3 is either totally or partially destroyed by acetolysis. Where it has been partially destroyed, its traces can be seen in places as small streaks or patches. In sections made from fresh material this layer, if present, remains intact and forms a very thin, homogeneous, sometimes granular layer or appears as a lens-shaped body at the apertures.

The presence of a well developed nexine 1 and the degree of its thickness have been interpreted as factors pointing towards the degree of 'evolution' of a species.

The absence of nexine 1 has been interpreted as pointing towards the 'primitiveness' of a species.

The presence of a well developed nexine 3 is tentatively assumed as pointing towards the 'primitiveness' of a species.

In contradistinction the absence of nexine 3 has been interpreted as pointing towards a more 'advanced' condition.

Accordingly the subfamily Mendoncioideae is regarded as 'primitive' and the subfamily Thunbergioideae more 'primitive' than Mendoncioideae. Within the Thunbergioideae *Thunbergia* is considered 'primitive', *Pseudocalyx* less 'primitive' and *Pounguia* more 'advanced'.

The subfamily Acanthoideae is regarded as an assemblage of

'primitive' and 'advanced' tribes. The tribes Justicieae, Odontonemeae, Hygrophileae, Asystasieae, Aphelandreae, Acantheae, Ruellieae, Petalidieae, Hygrophileae and Trichanthereae are considered more 'advanced' than the tribes Strobilantheae, Barlerieae and Andrographideae.

It has been found that exine stratification is a further proof of a porate status having evolved from a spirotrema via a colporate and a colpate status.

On the basis of pollen morphology the following suggestions are made:

The transfer of Nelsonioideae to the Scrophulariaceae is justified.

Mendoncioideae and Thunbergioideae being made into separate families, Mendonciaceae and Thunbergiaceae, is an improvement in the classification.

Gilletiella should be removed from the Mendoncioideae and included in the Acantheae.

The suggestion to exclude *Poungia* from Thunbergioideae and include it in Whitfieldieae is not justified.

Meyenia should probably be excluded from Thunbergioideae and included in the Pedaliaceae.

The suggestion to reduce Louteridieae to a subtribe of the Ruellieae does not seem to be justified.

Forsythiopsis is probably congeneric with *Ruttya*.

Barlerieae and Ruellieae are not closely related.

Acantheae and Aphelandreae show a close affinity.

Rhombochlamydeae should be retained as an independent tribe.

Thomandersia should be excluded from Asystasieae and included in the Pedaliaceae.

Rungia should be excluded from Odontonemeae and included in Justicieae.

Rhytiglosseae does not show any affinity to Trichanthereae and *Rhacodiscus* should be retained in the former.

The pollen grains of *Poikilacanthus* are not "alveolate" and do not resemble those of Ruelliinae.

The suggestion to unite *Glockeria* and *Habracanthus* is not supported by pollen morphology.

Fossil pollen grains from the Tertiary (i.e. the Miocene) have been found to resemble those of *Ruellia*, *Hulemacanthus*, *Sanchezia*, etc.

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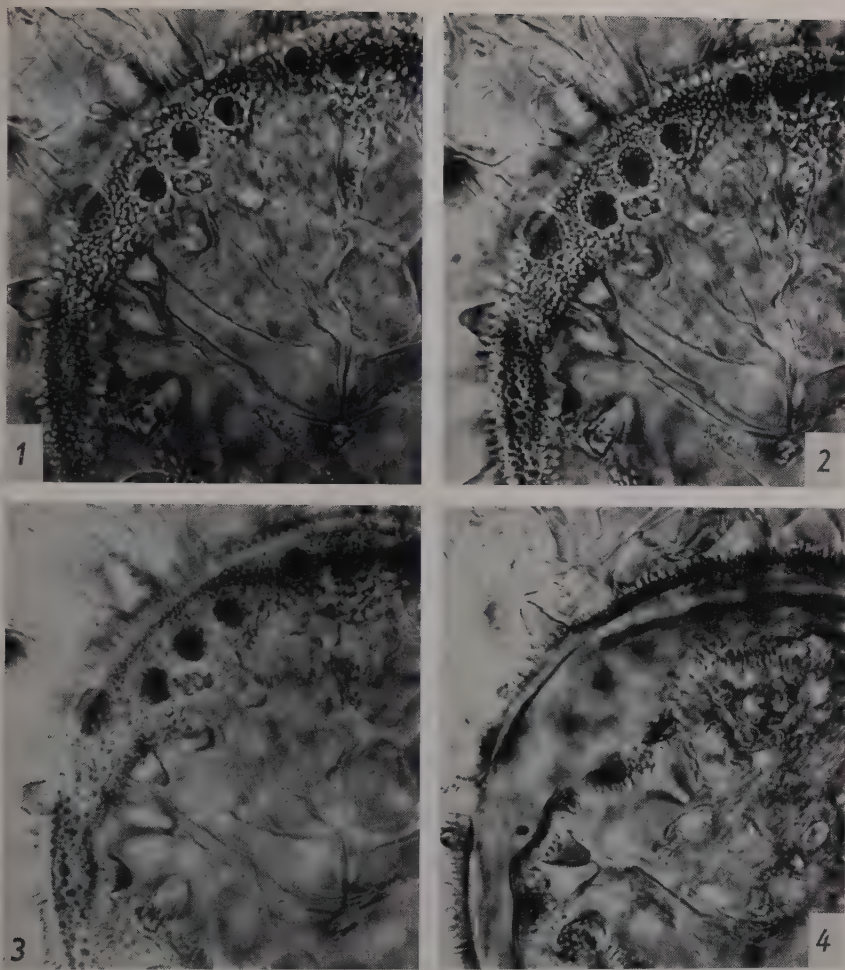


Plate 1. Figs. 1-4. *Acanthopale* sp. ($\times 1000$). — 1, small processes (white) and blunt spines (dark); 2 and 3, the small processes turn dark; small rod-like structures appear at the base of the spines; they are more clearly seen in the optical section; 4, optical section.

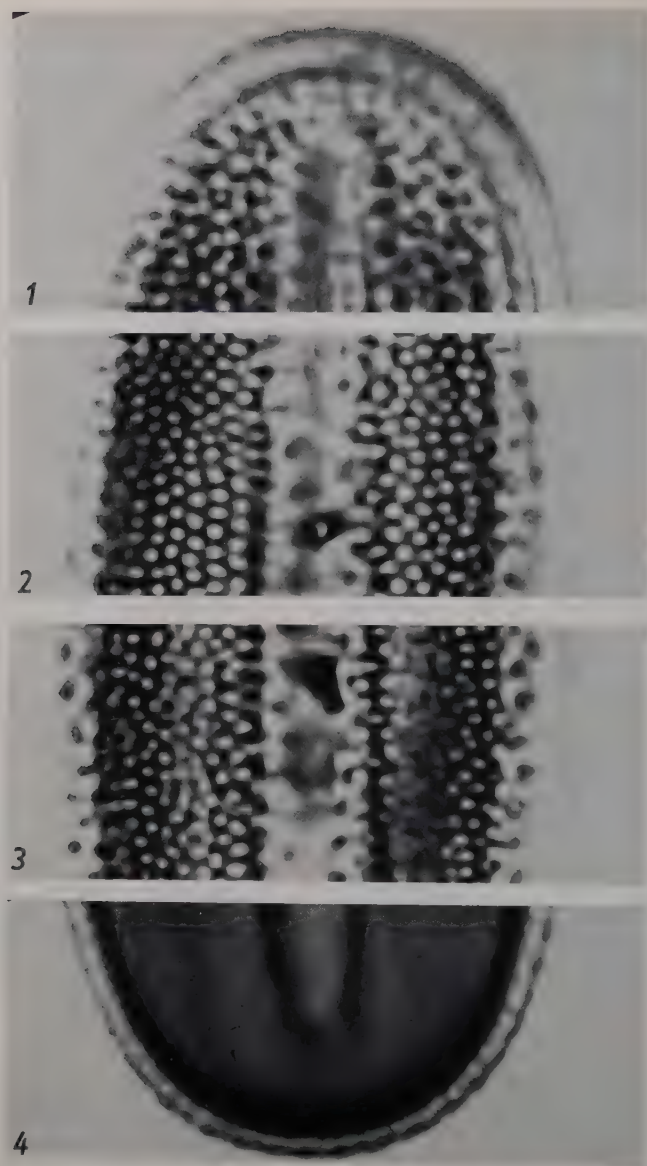
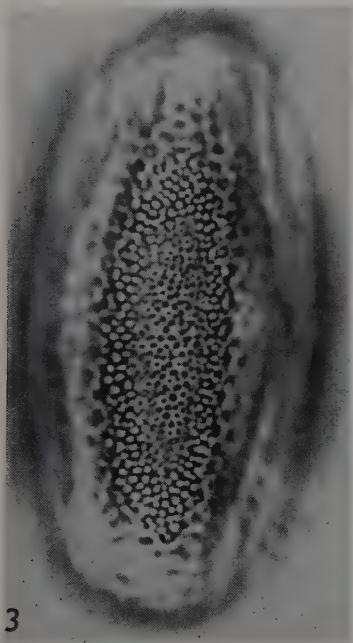
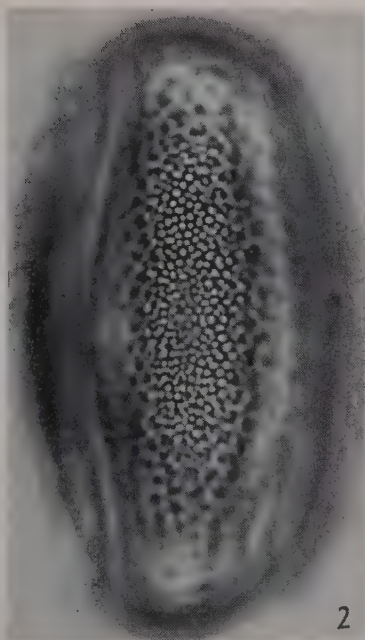
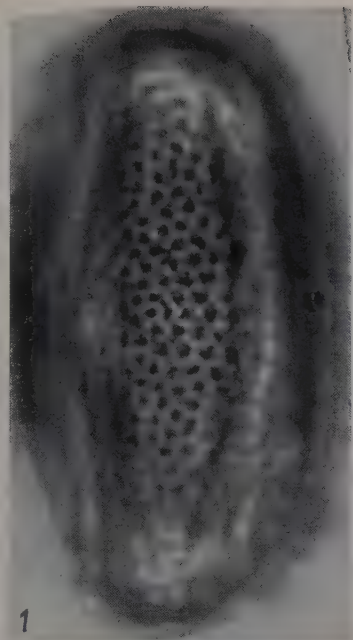


Plate 2. Figs. 1-4. *Acanthus arboreus* Forsk. ($\times 3000$; enlarged from $\times 1000$). — 1, homobrochate reticulum; 2 and 3, muri break up into a simplibaculate pattern, at a still lower focus the bacula turn dark; 4, optical section.

Plate 3. Figs. 1-4. *Acanthus ilicifolius* L. ($\times 1000$). — 1, homobrochate reticulum; 2, muri break up into a simplibaculate pattern; lumina provided with bacula; 3, (central part) bacula turn dark; 4, optical section.



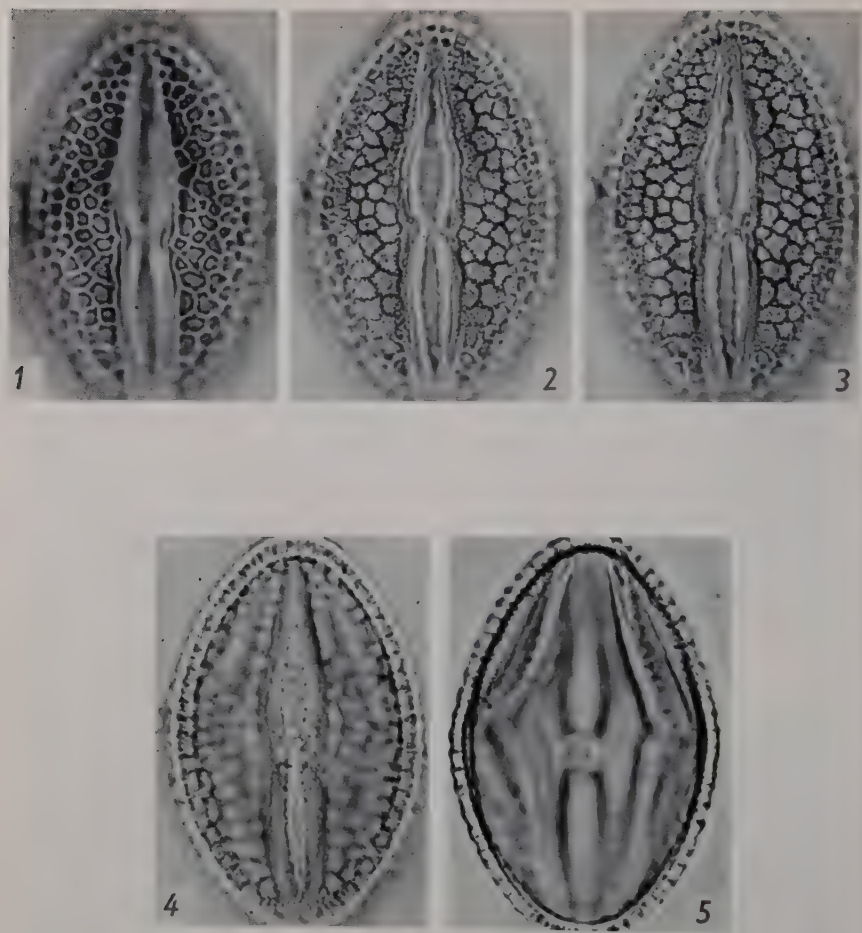
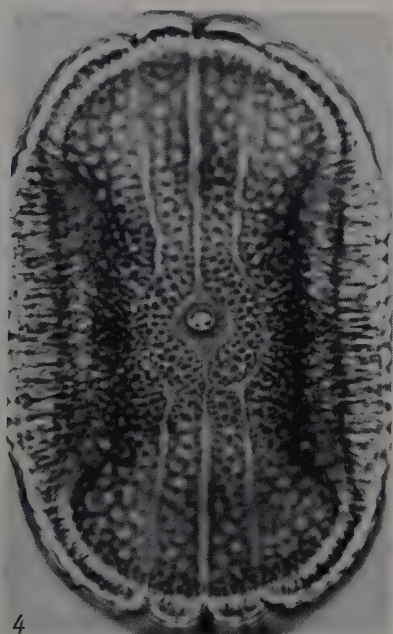
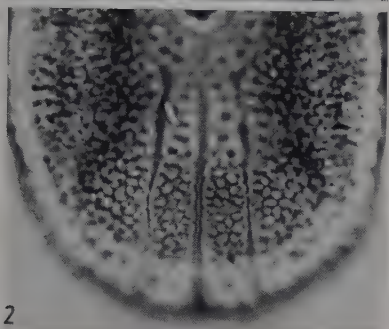
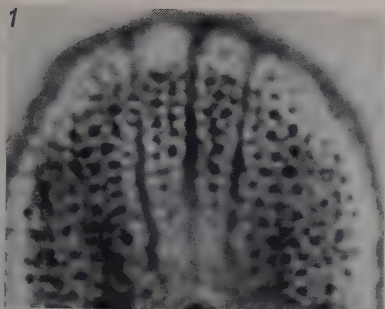


Plate 4. Figs. 1-5. *Andrographis echioides* Nees ($\times 1000$). — 1, homobrochate reticulum; 2, muri break up into a simplibaculate pattern; luminal bacula appear as white dots; 3, 4, the bacula turn dark; 5, optical section.

Plate 5. Figs. 1-5. *Asystasia coromandeliana* Nees ($\times 1000$). — 1, reticulum; 2, muri break up into a simplibaculate pattern; 3, mural bacula turn dark; small processes appear along the contour of the pore; arrangements of colpoid streaks and bands can also be seen; 5, optical section showing, i.e., the characteristic thickened equatorial part of the nexine.



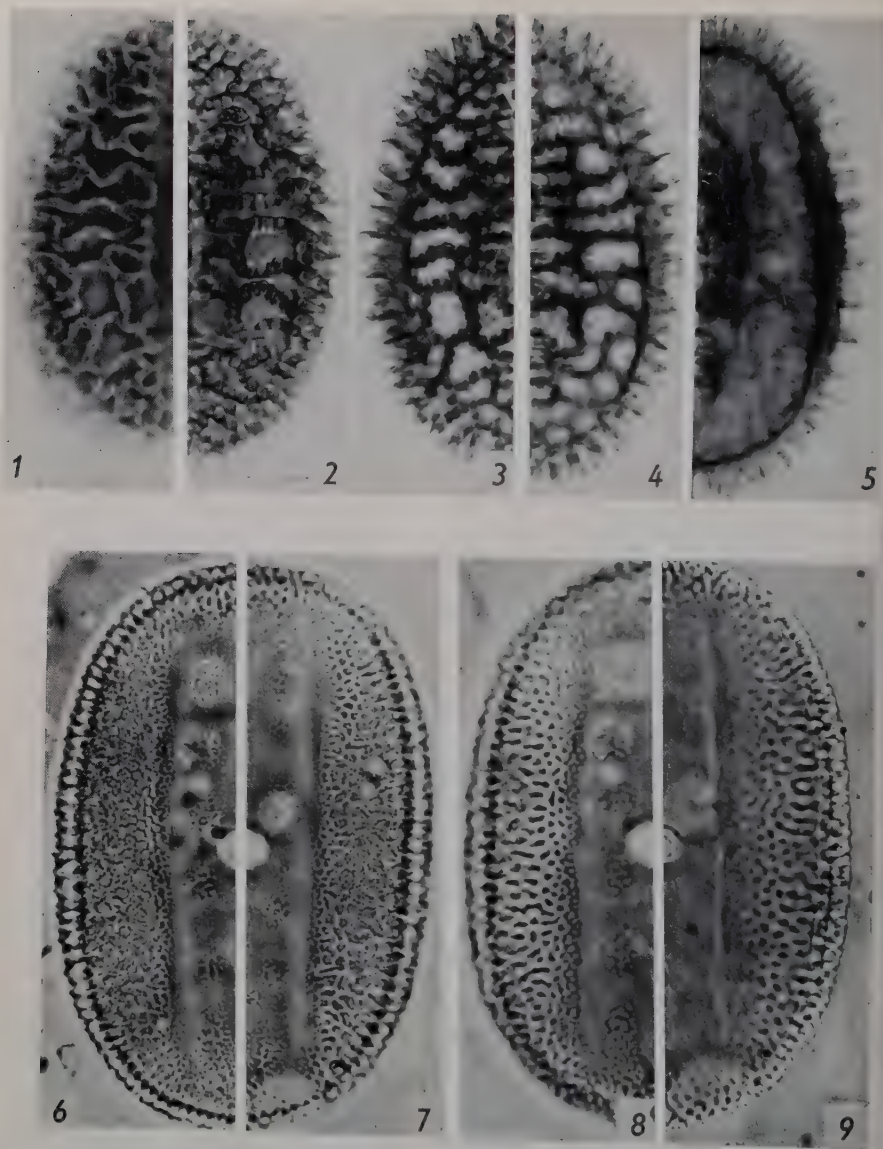


Plate 6. Figs. 1-5. *Barleriola multiflora* Urb. ($\times 1000$). — 1, heterobrochate reticulum and winding muri; 2, muri break up into a simplibaculate pattern; 3, bacula turn dark; luminal processes appear as white dots; 4, luminal processes turn dark; 5, optical section. Figs. 6-9. *Beloperone californica* Benth. ($\times 1000$). — 6, punctitegillate pattern in peripheral part of the figure; in the "trema area" more or less rounded insulae with reticulate pattern; 7, puncta distinctly seen as dark dots around the bacula; 8, puncta at least in some places appearing as white dots around the dark bacula; 9, optical section.

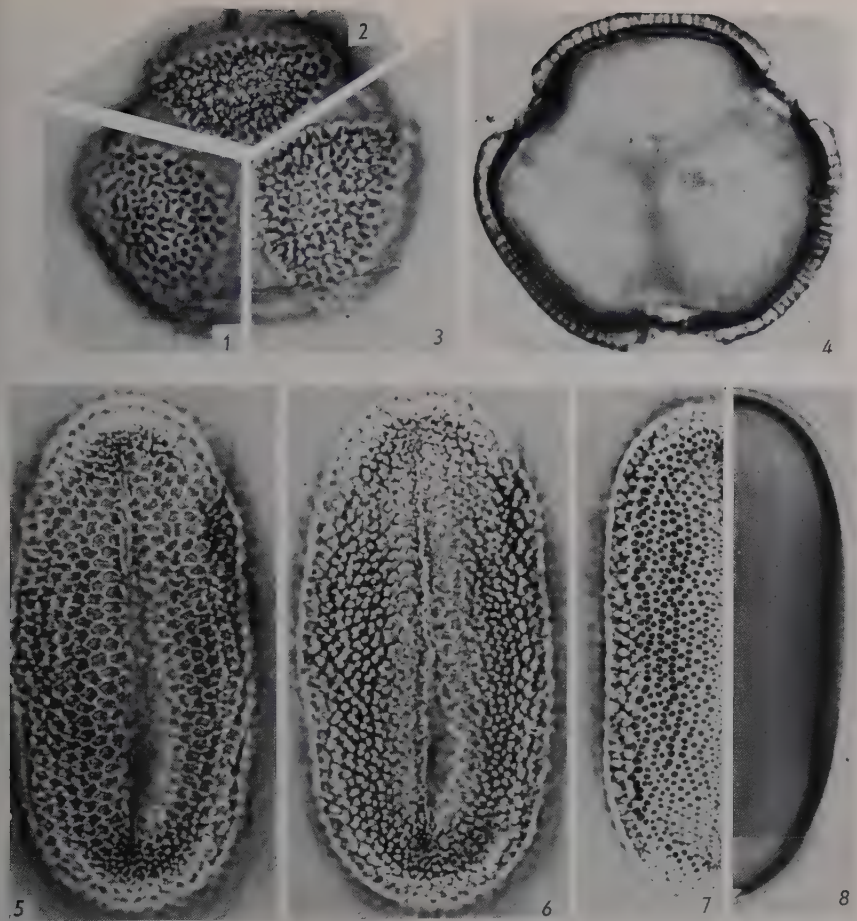


Plate 7. Figs. 1-4. *Blechum brownei* Juss. ($\times 1000$; reduced from $\times 1500$). — 1, homobrochate reticulum; 2, muri break up into a simplibaculate pattern; 3, bacula bases turn dark; 4, optical section. Figs. 5-8. *Blepharis boerhaviaefolia* Pers. ($\times 1000$; reduced from $\times 1500$). — 5, homobrochate reticulum; 6, muri break up into a simplibaculate pattern; a narrow colpus with uneven margins can also be seen; 7, bacula bases turn dark; 8, optical section.

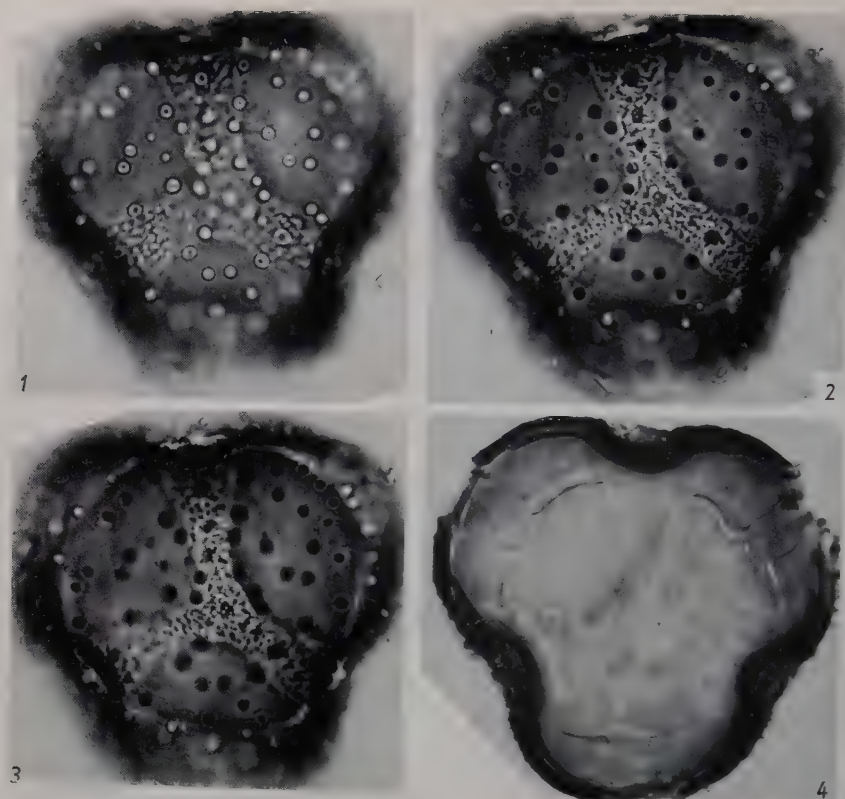


Plate 8. Figs. 1-4. *Brachystephanus africanus* S. Moore ($\times 1000$; reduced from $\times 1200$). — 1, verrucae appear as white dots; band-shaped depressions with densely spaced, small processes; 2 and 3, verrucae and small processes dark; 4, optical section.

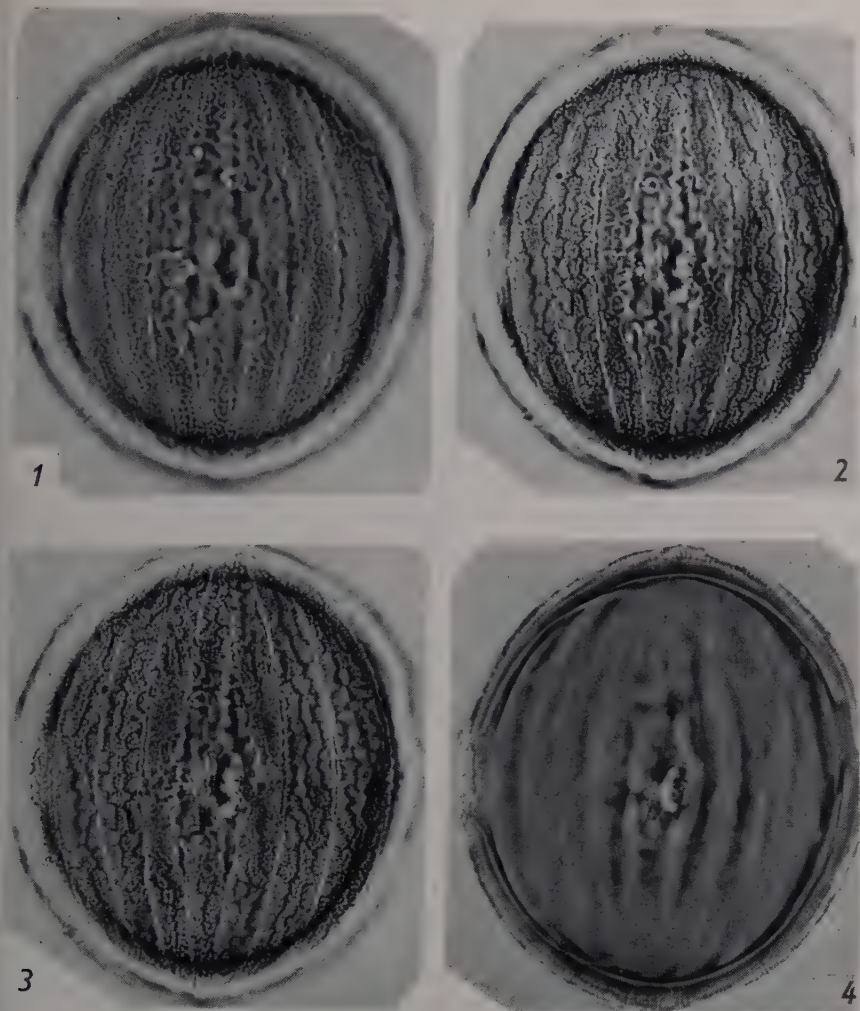


Plate 9. Figs. 1-4. *Brillantaisia emini* Lindau ($\times 1000$). — 1, suprathegillar reticulum; 2, the same turns dark; infrathegillar bacula bright; 3, the latter turn dark; 4, optical section.

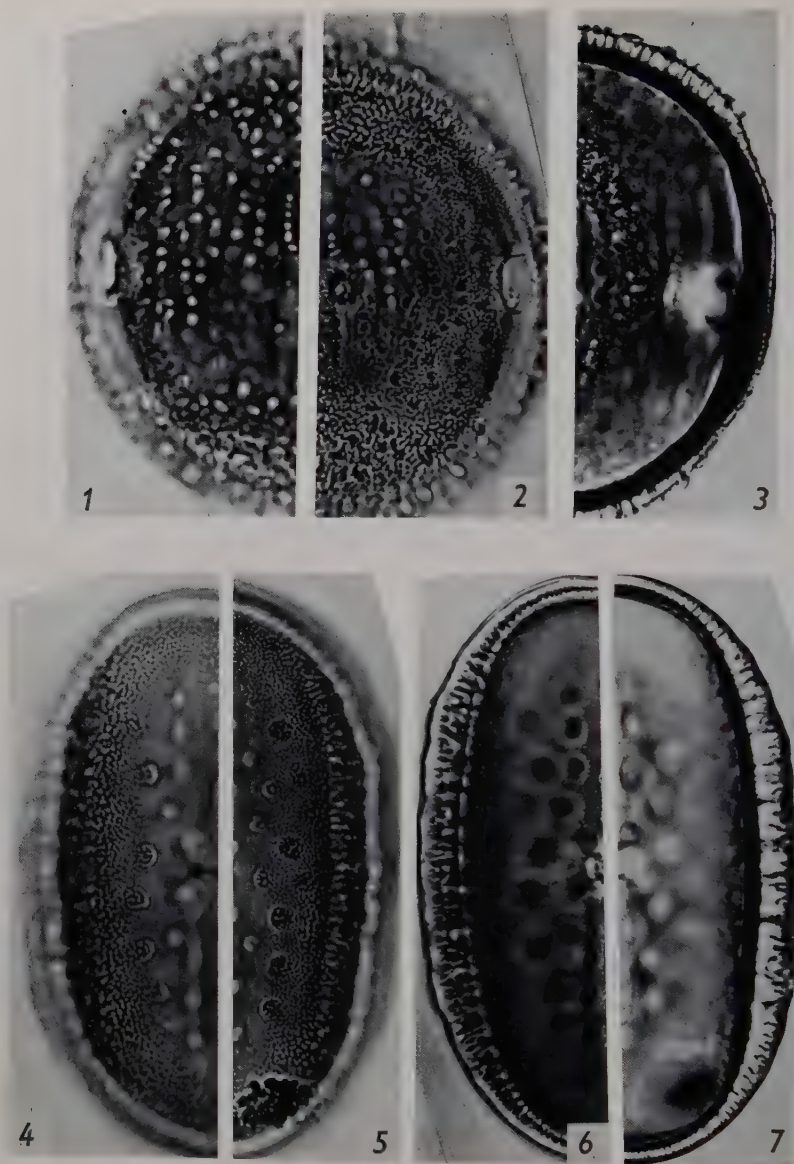


Plate 10. Figs. 1-3. *Chlamydocardia buettneri* Lindau ($\times 1000$). — 1, blunt, supratrigillar processes (bright); 2, the processes turn dark; small, infratrigillar bacula bright; 3, optical section. Figs. 4-7. *Jacobinia carnea* (Lindl.) Nichols. ($\times 1000$). — 4, insulae and bacula in "peripheral area"; 5, insulae and bacula turn dark; 6, wavy ectosexine with branched bacula; 7, optical section.

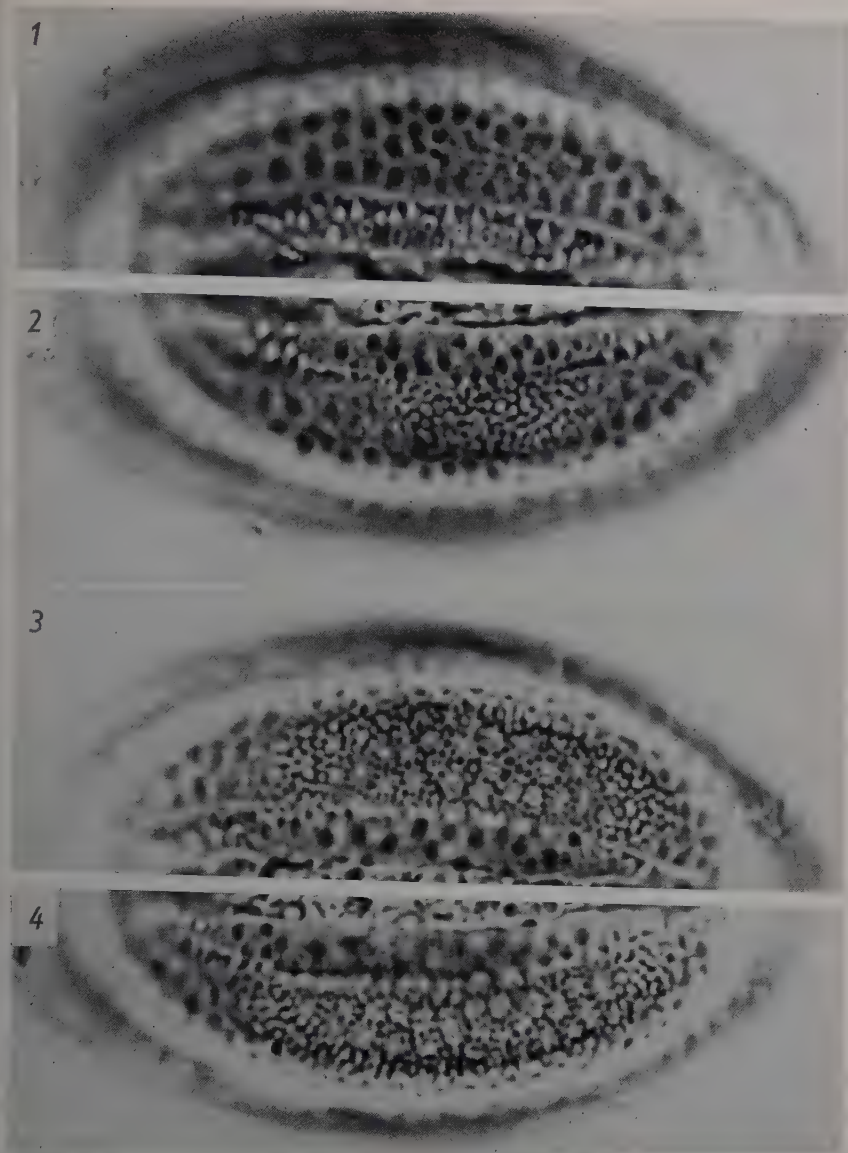


Plate 11. Figs. 1-4. *Cystacanthus turgidus* Nichols. ($\times 2000$). — 1, homobrochate reticulum; 2, processes at colpi margins turn dark; 3, bacula (white and grey dots) appear in the lumina; 4, the dots turn dark. — Polar axis horizontal.

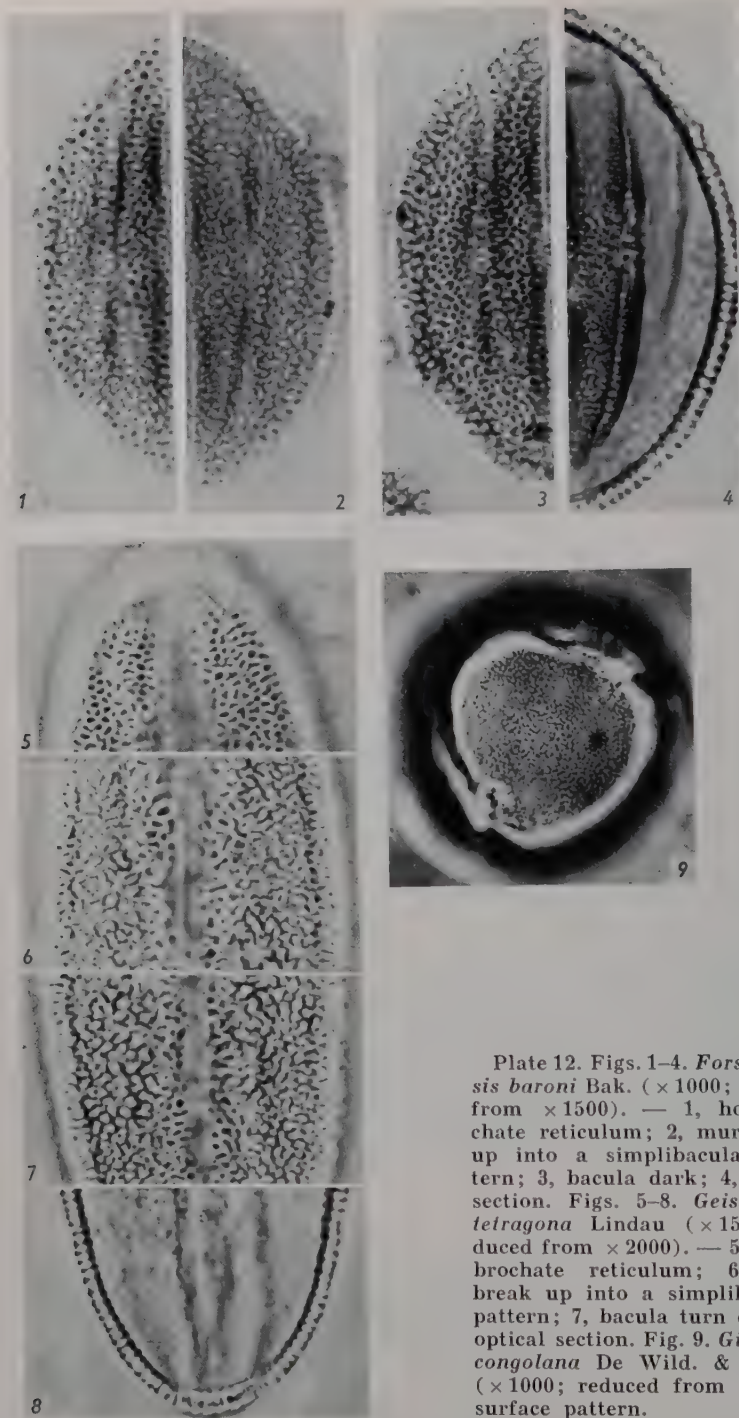


Plate 12. Figs. 1-4. *Forsthiopsis baroni* Bak. ($\times 1000$; reduced from $\times 1500$). — 1, homobrochate reticulum; 2, muri break up into a simplibaculate pattern; 3, bacula dark; 4, optical section. Figs. 5-8. *Geissomeria tetragona* Lindau ($\times 1500$; reduced from $\times 2000$). — 5, homobrochate reticulum; 6, muri break up into a simplibaculate pattern; 7, bacula turn dark; 8, optical section. Fig. 9. *Gilletiella congolana* De Wild. & Durand ($\times 1000$; reduced from $\times 1500$), surface pattern.

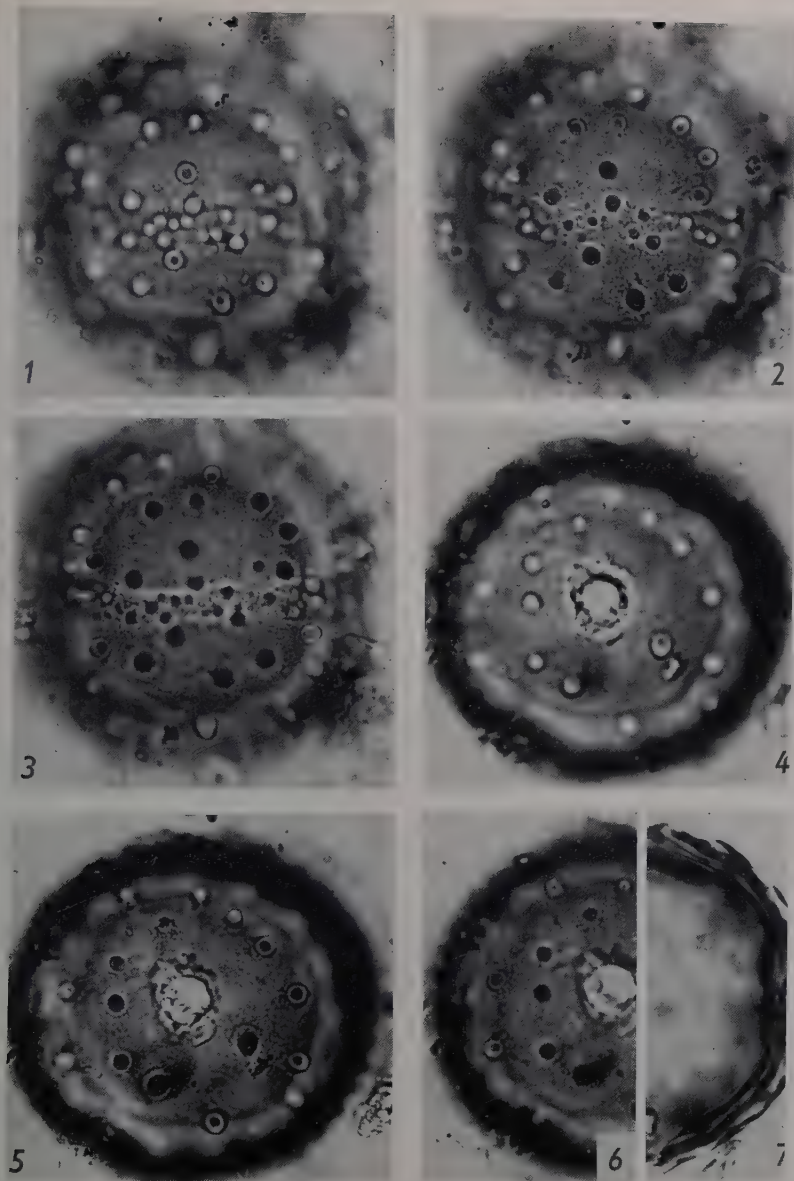


Plate 13. Figs. 1-7. *Glockerella gracilis* Nees ($\times 1000$). — Figs. 1-3, polar view; Figs. 4-7, equatorial view. — 1, spinuloid processes and slightly depressed colpoid streak; 2 and 3, processes turn dark; 4, processes (bright) and circular pore; 5, 6, processes dark; 7, optical section.

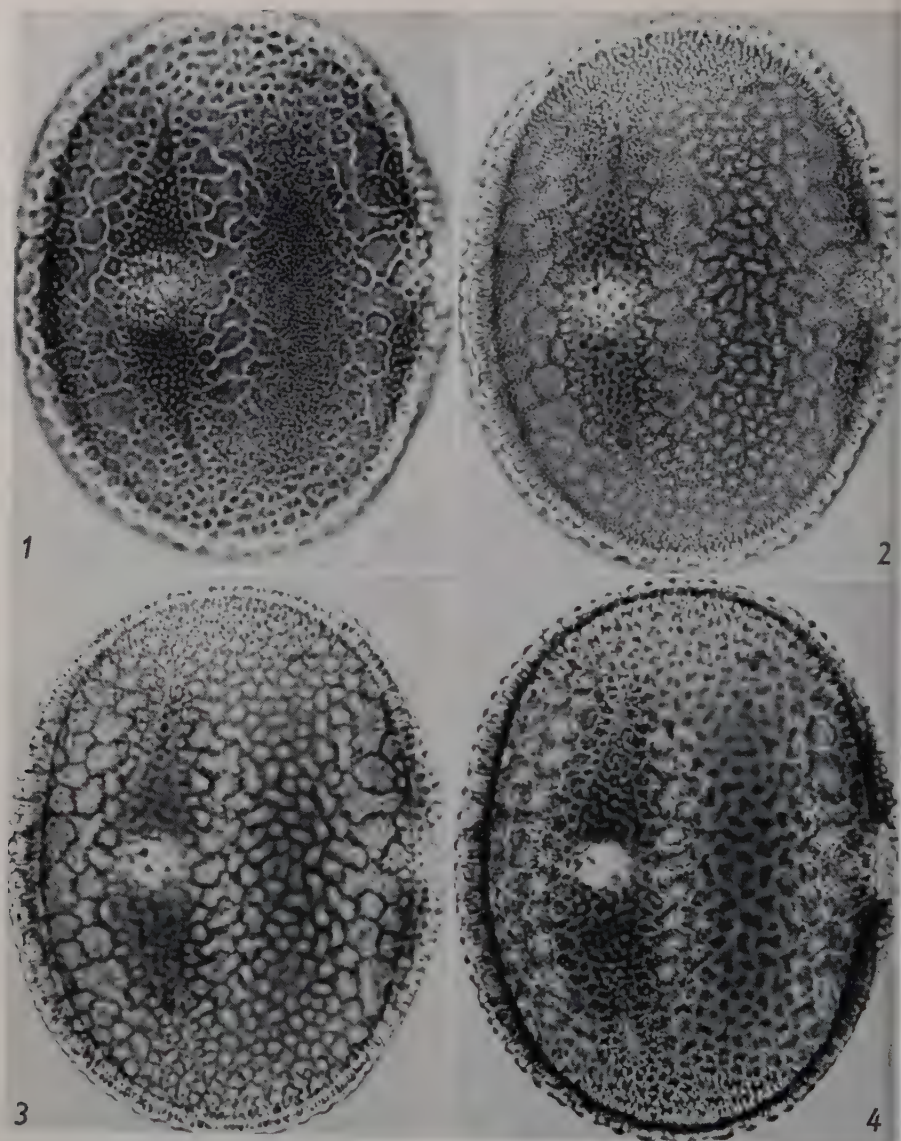


Plate 14. Figs. 1-4. *Hulemacanthus whitei* S. Moore ($\times 1000$). — 1 (central part), heterobrochate reticulum with bright muri; 2, muri dark, duplibaculate; luminal bacula dark; bacula near poles bright; 3, bacula near poles dark; 4, optical section and pattern on the opposite side. — Cf. also Pl. 41, Fig. 3.



Plate 15. Figs. 1-5. *Hypoestes antennifera* S. Moore ($\times 1000$). — 1, puncta in peripheral area very small, dark; central, solid part of bacula bright; 2, most of the puncta bright; 3, most of the puncta out of focus; main part of bacula slightly darker than interbacular interstices; 4, base of bacula very dark, os clearly seen; 5, optical section. Explanatory diagram and section, see Pl. 42, Fig. 2.

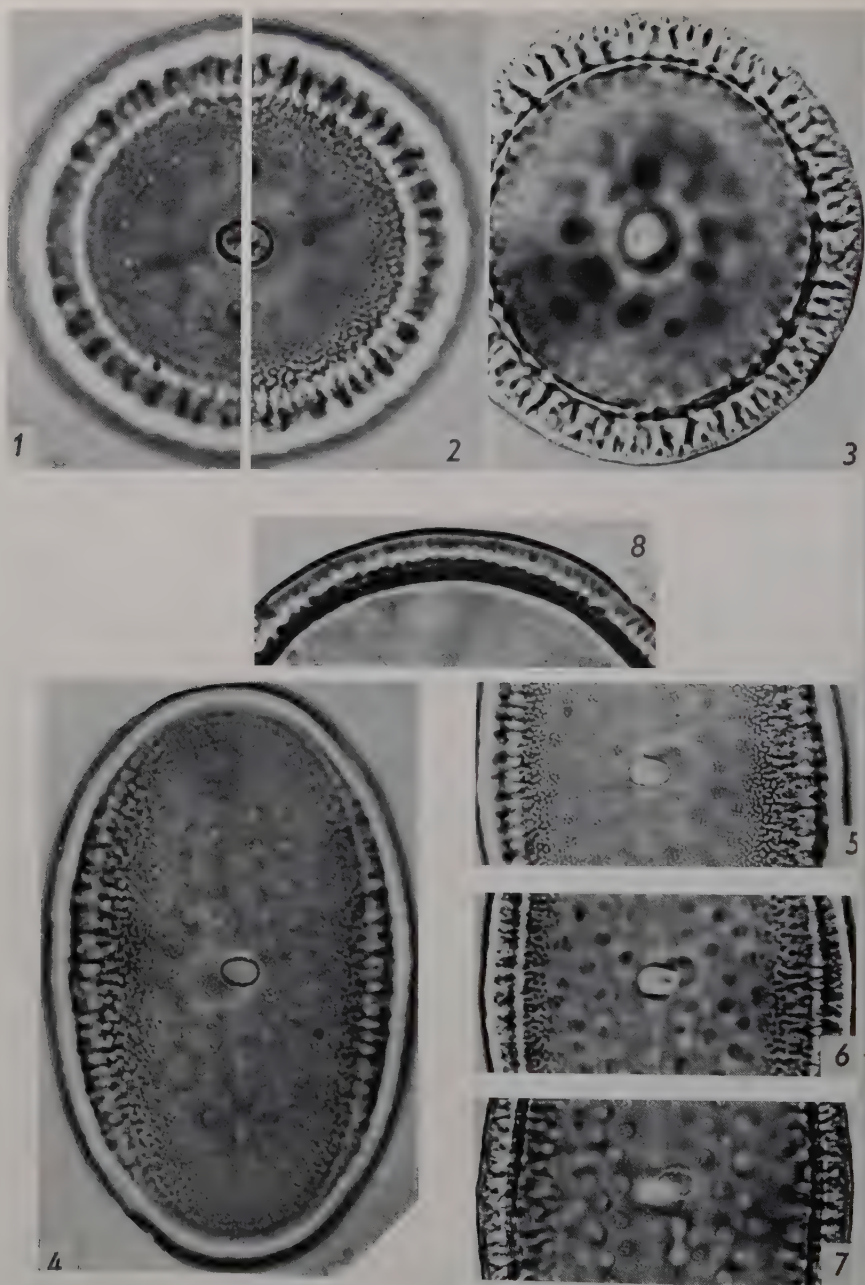


Plate 16. Figs. 1-3. *Rhytiglossa lactea* (Lindau) ex Engl. ($\times 1500$). — 1, low, indistinct, tegillar processes bright; 2, some puncta (dark) and bacula (bright) seen; 3, optical section. Figs. 4-8. *Jacobinia carnea* (Lindl.) Nichols. ($\times 1000$). — 4, longitudinal pore and insulae in the "trema area"; 5, 6, the same under different foci; 7, pore and insulae on the opposite side; 8, optical section ($\times 2000$).

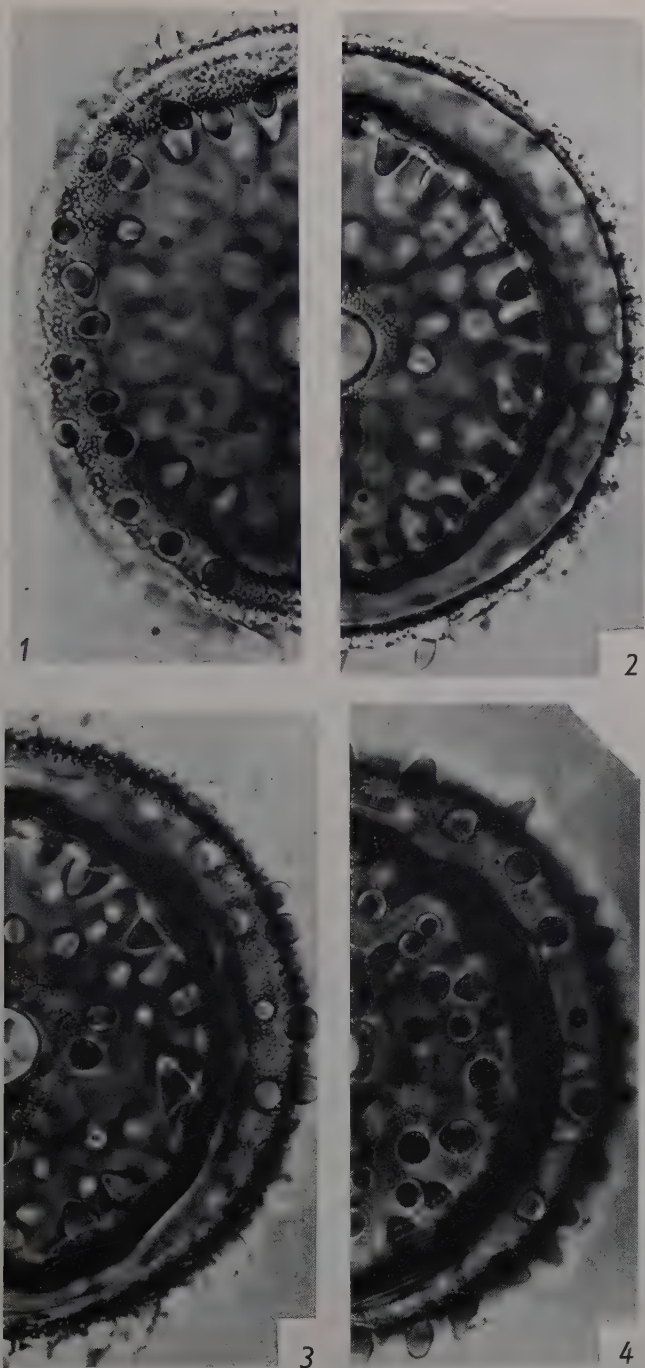


Plate 17. Figs. 1-4. *Kalbreyerella rostellata* Lindau ($\times 1000$). — 1, blunt spines (dark) and small bacula (bright); 2, optical section (right margin); 3, and 4, lower foci. — Cf. also Pl. 40, Fig. 5.

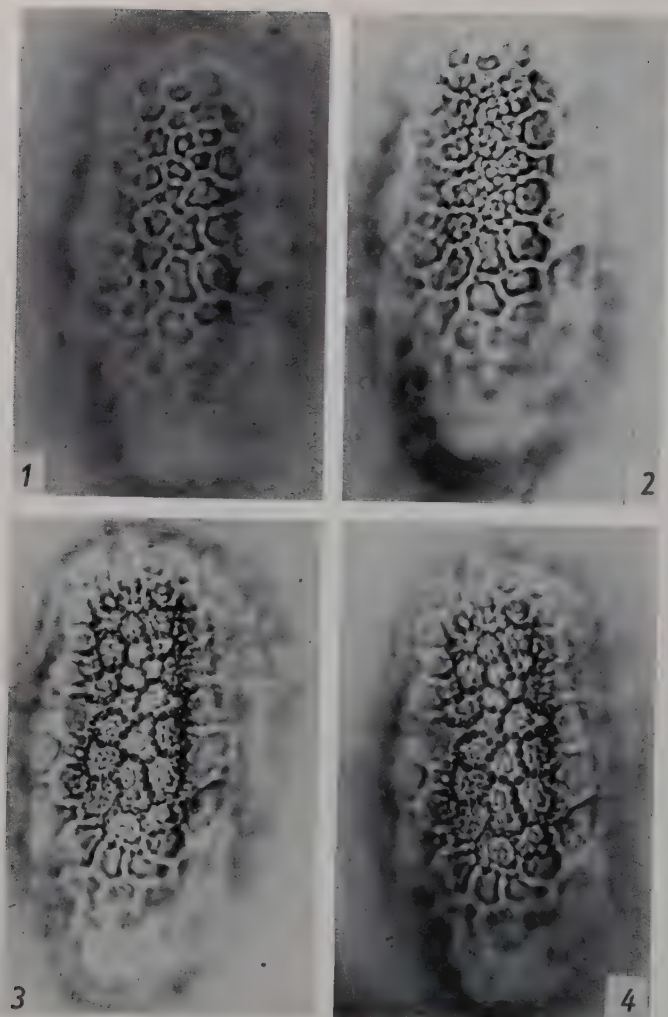


Plate 18. Figs. 1-4. *Lophostachys falcata* Nees ($\times 1000$). — 1, slightly heterobrochate reticulum; 2, the muri break up into a simplibaculate pattern; lumina with densely spaced bacula; 3, 4, the same under lower foci.

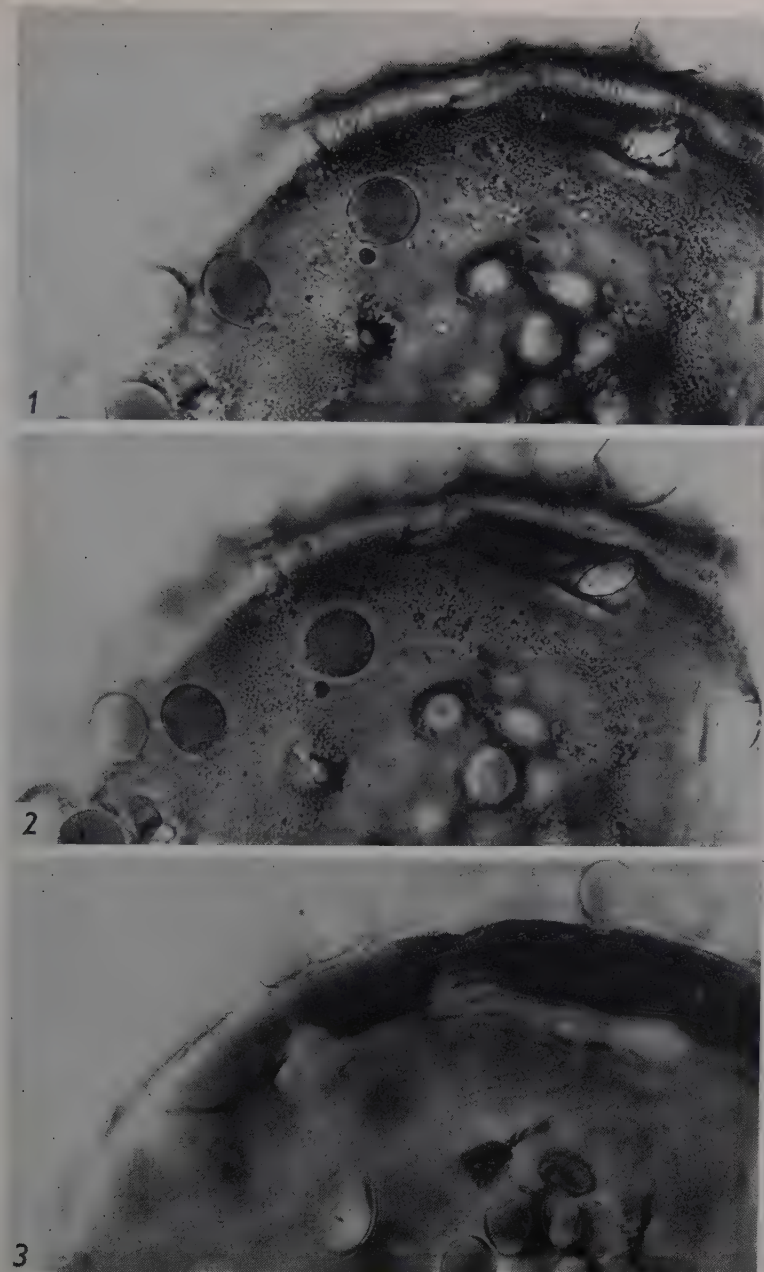


Plate 19. Figs. 1-3. *Louteridium donnell-smithii* Wats. ($\times 1000$). — 1, pore in upper right corner; small processes (bright); gemmae; 2, the same under lower focus; 3, optical section showing thick nexine and very thin tegillum supporting two gemmae.

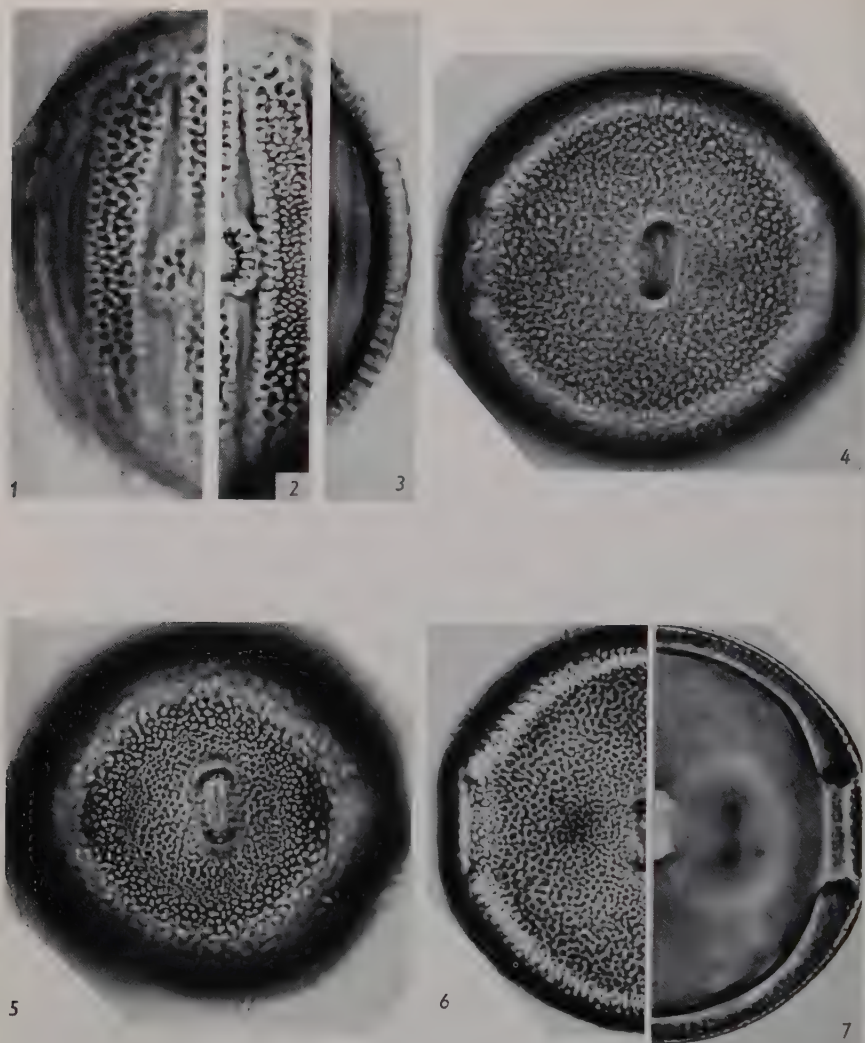


Plate 20. Figs. 1-3. *Melleria lobulata* S. Moore ($\times 1200$; reduced from $\times 1500$). — 1, homobrochate reticulum and colpoid streak; 2, muri break up into a simplibaculate pattern and a collar-like, sexinous patch around the aperture; 3, optical section. Figs. 4-7. *Mendoncia aspera* (R. & P.) Nees ($\times 1000$; reduced from $\times 1500$). — 4, the punctitegillate condition of the sexine is shown; colpus short, slit-like; 5, 6, the same under lower foci; 7, optical section.

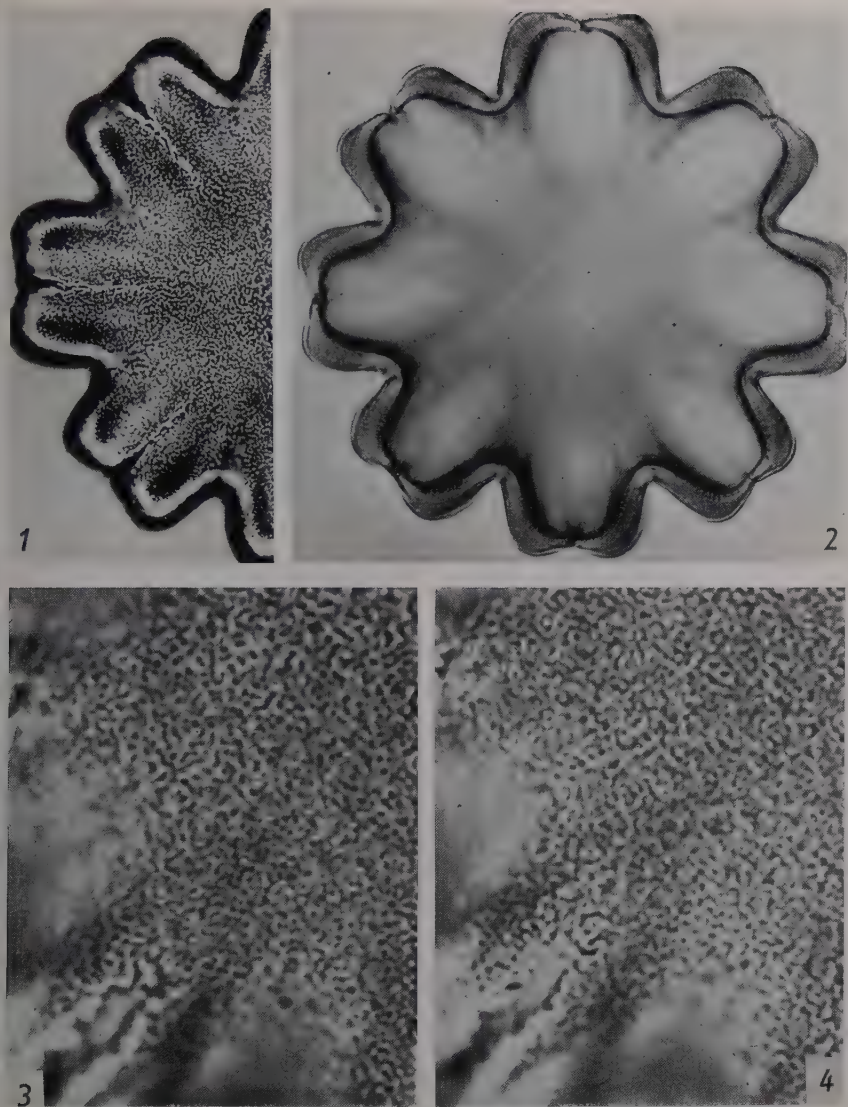


Plate 21. Figs. 1-4. *Meyenia hawtayneana* Wall. ($\times 1000$). — 1, part of a pollen grain in polar view showing colpi and mesocolpial concavities; 2, optical section; 3, 4 ($\times 1500$), surface pattern.

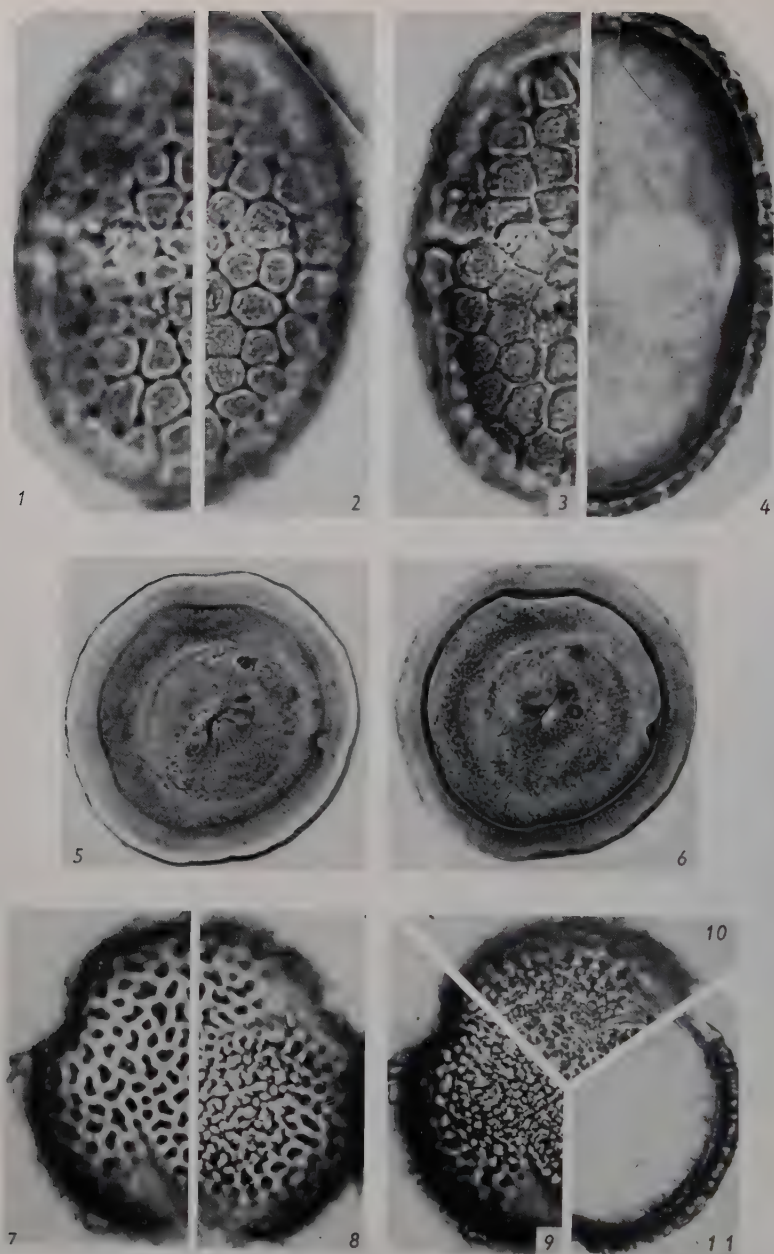


Plate 22. Figs. 1-4. *Poikilacanthus gilliesii* Lindau ($\times 1000$; reduced from $\times 1500$). — 1, polygonal, densely spaced insulae; 2, 3, the same under lower foci; 4, optical section showing nexine and faint outline of three pores. Figs. 5, 6. *Pounguia purpurata* R. Ben. ($\times 1000$; reduced from $\times 1500$). — 5, showing central, circular, weak zone; 6, optical section showing nexine and a single outgrowth from the same. Figs. 7-11. *Pseuderanthemum malaccense* Lindau ($\times 1000$; reduced from $\times 1200$). — 7, homobrochate reticulum; 8, muri break up into a simplibaculate pattern; 9, 10, the same under different foci; 11, optical section.

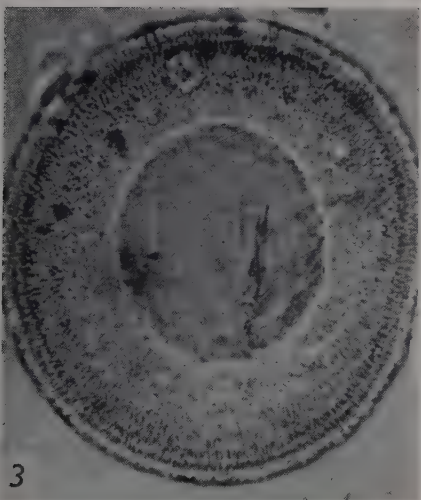
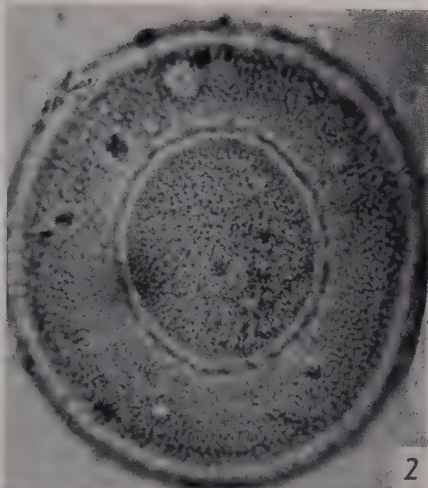
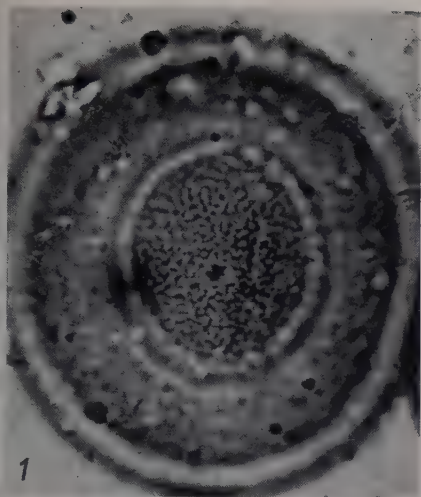


Plate 23. Figs. 1-4. *Pseudocalyx africanus* S. Moore ($\times 1200$). — 1, part of exine surrounded by a weak aperture zone (N.B. the pollen grains are usually spirotreme); 4, optical section.

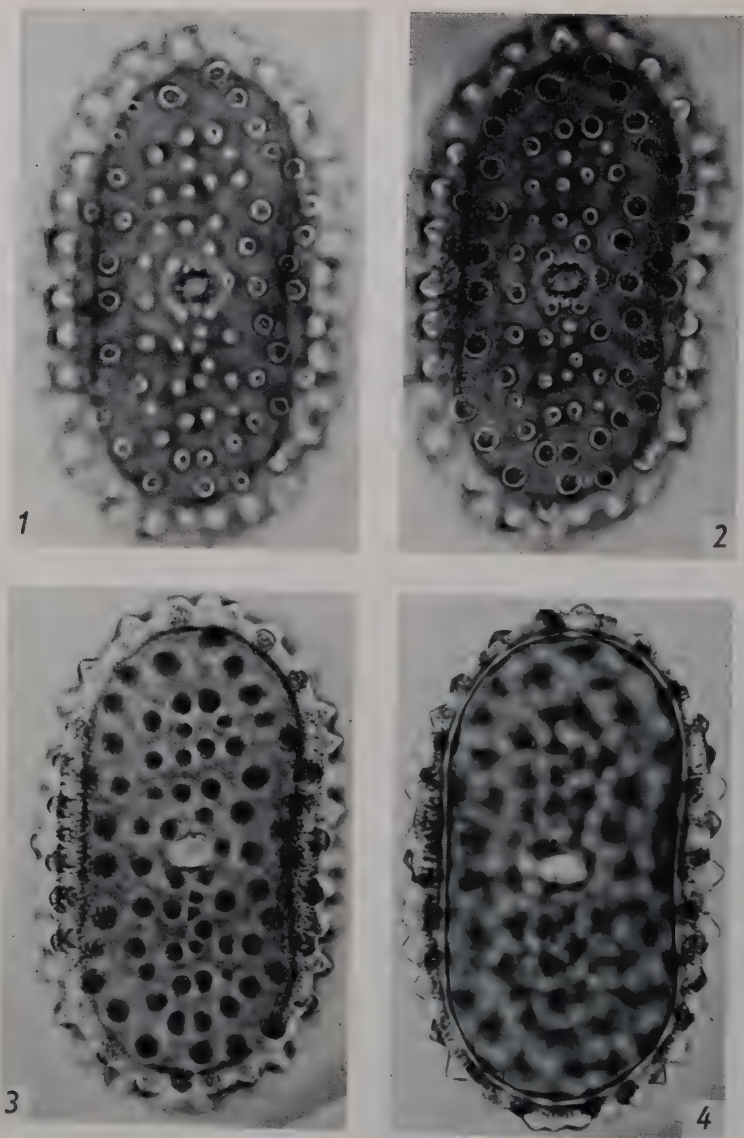


Plate 24. Figs. 1-4. *Rhacodiscus calycinus* (Nees) Brem. ($\times 1000$). — 1, pollen grain with central pore, densely granular pore membrane and verrucae, each with a small hollow; 2, 3, the same under lower foci; 4, optical section.

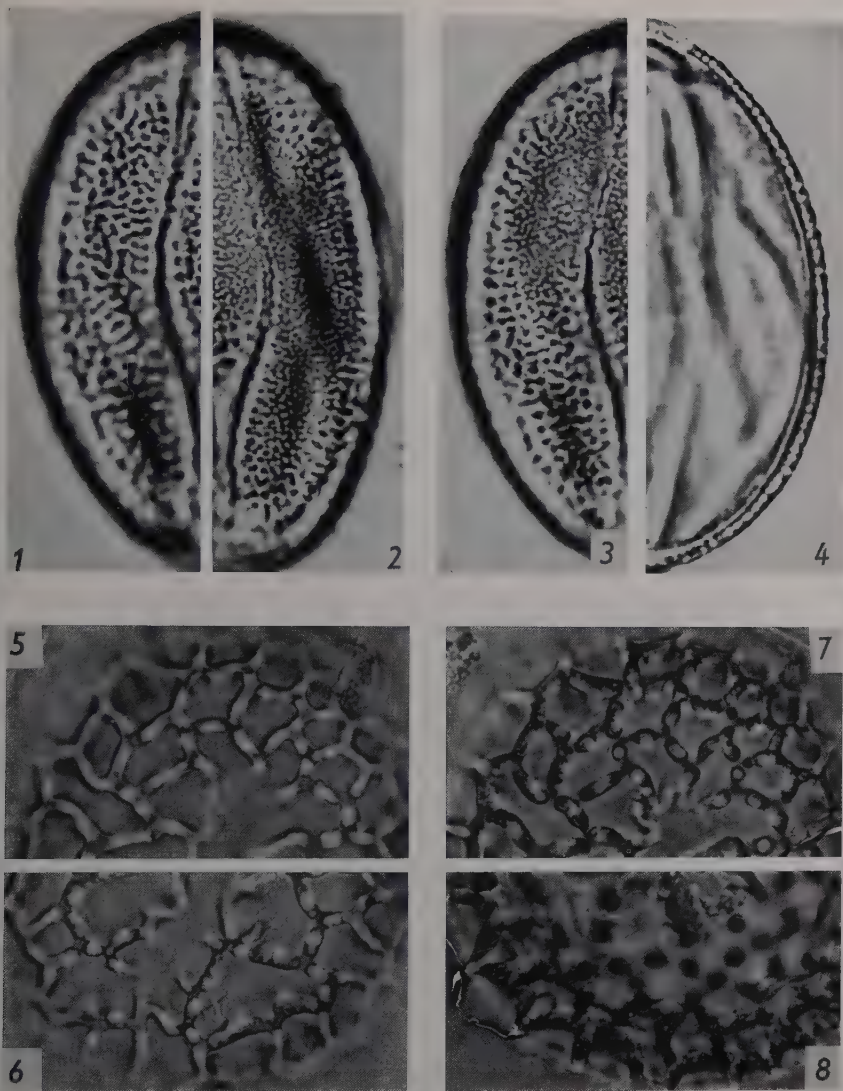


Plate 25. Figs. 1-4. *Rhombochlamys elata* Lindau ($\times 1500$). — 1, homobrochate reticulum and part of colpus (with incrassate membrane); 2, muri break up into a simplibaculate pattern; 3, the same under lower focus; 4, optical section. Figs. 5-8. *Ruellia angustiflora* Nees ($\times 1000$). — 5, homobrochate reticulum; 6, muri break up into a simplibaculate pattern; 7, 8, the same under different foci.

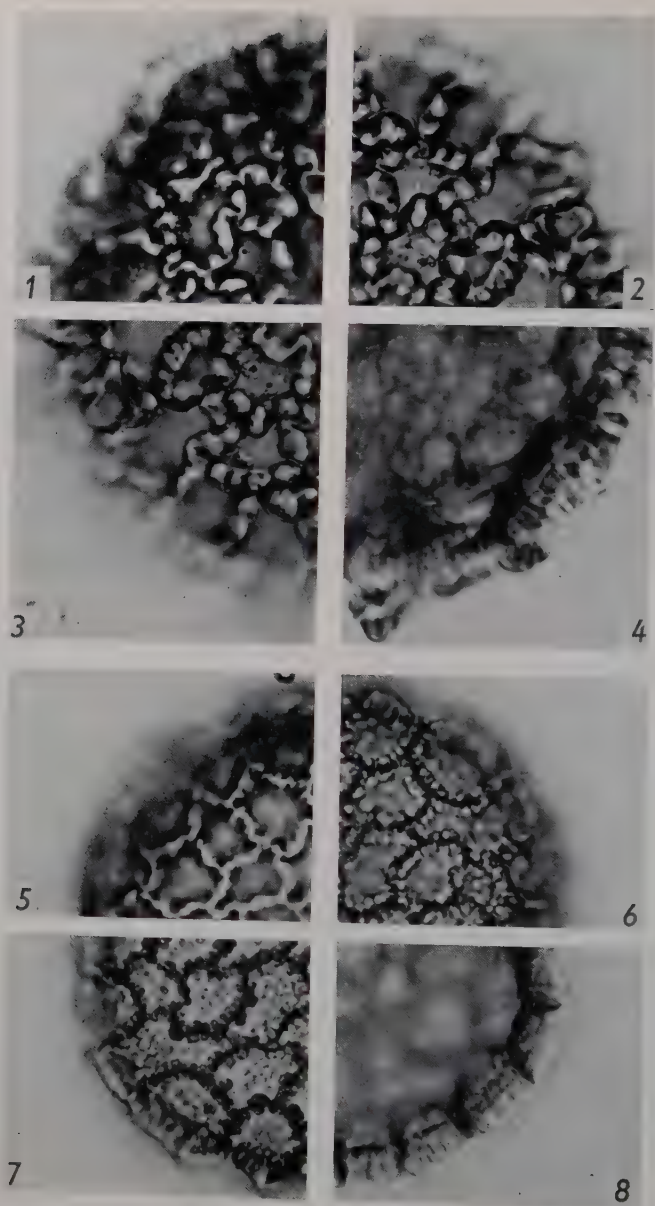


Plate 26. Figs. 1-4. *Ruellia brachysiphon* (Nees) Lindau ($\times 1000$). — 1, homobrochate reticulum; 2, muri break up into a simplibaculate pattern; 3, traces of luminal bacula can be seen; 4, optical section. Figs. 5-8. *Ruellia graecizans* Backer ($\times 1000$). — 5, homobrochate reticulum; 6, muri break up into a dupli-baculate pattern; 7, mural, infrategillar bacula dark; luminal bacula bright; 8, optical section.

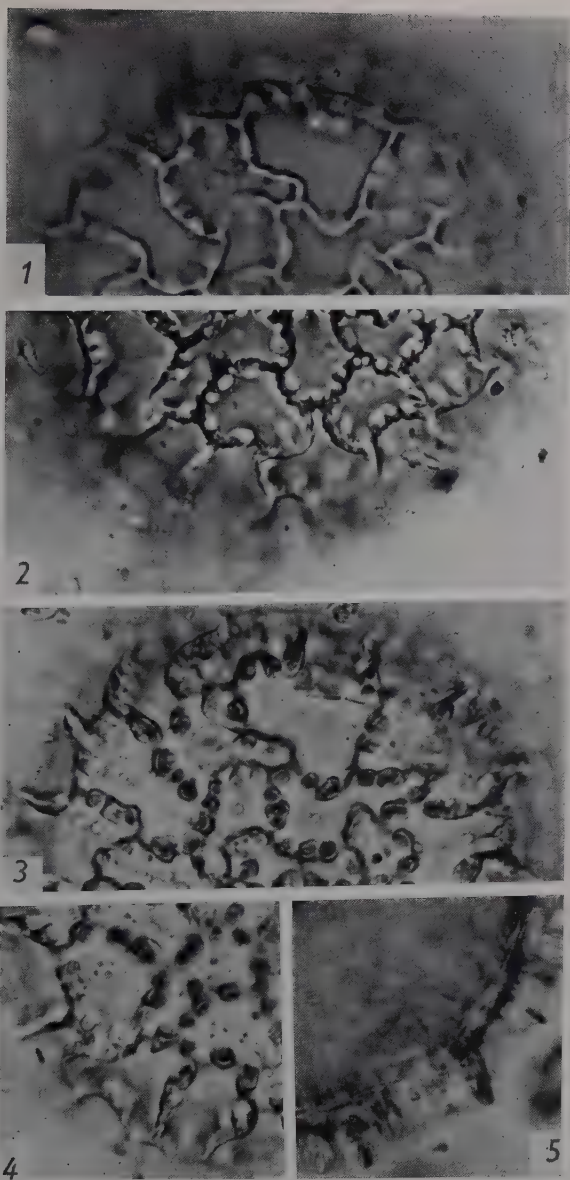


Plate 27. Figs. 1-5. *Ruellia pacifica* Svens. ($\times 1000$). — 1, homobrochate reticulum; 2, muri break up into a simplibaculate pattern; 3, mural, infrategillar bacula dark; 4, small, scattered luminal bacula bright; 5, optical section.

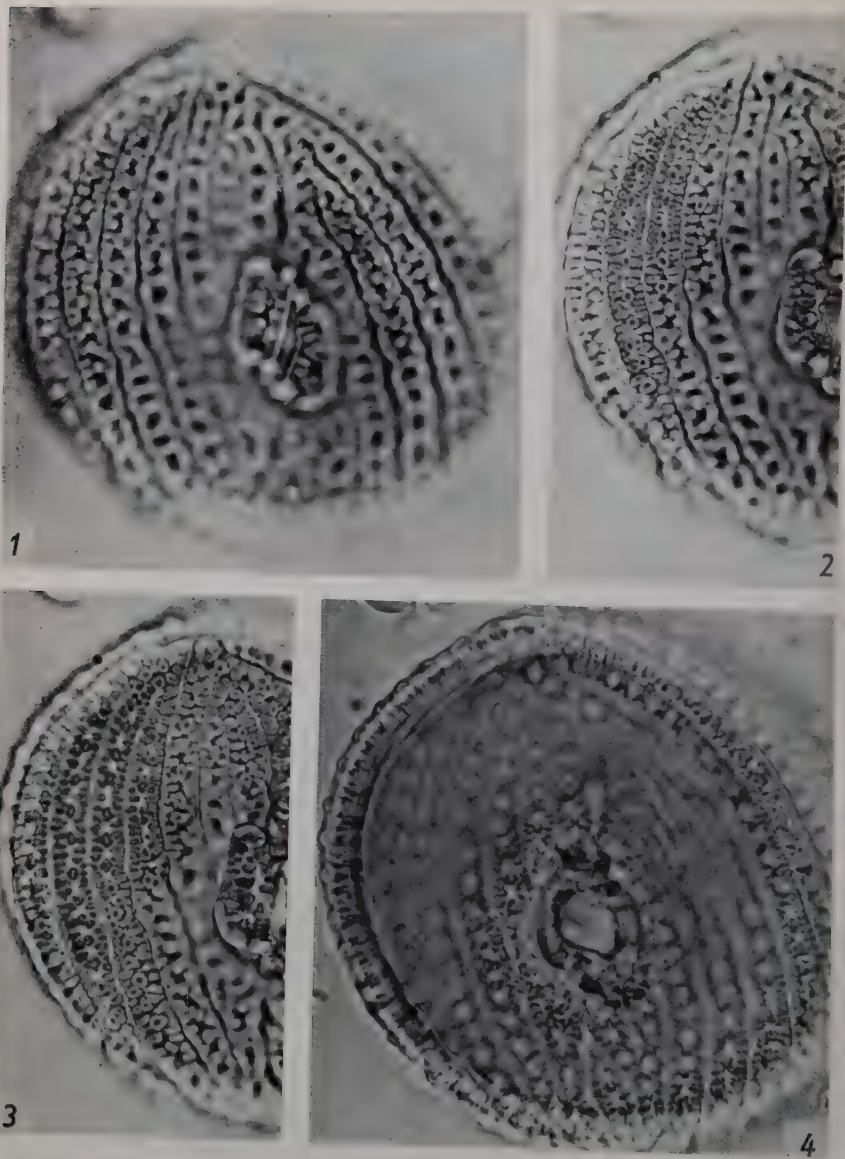
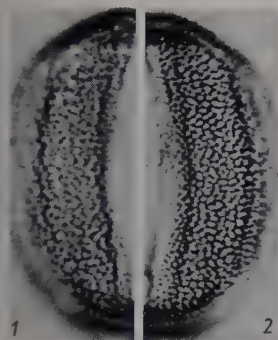
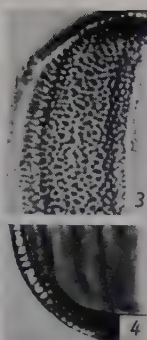


Plate 28. Figs. 1-4. *Sanchezia klugii* Leonard ($\times 1000$). — 1, homobrochate reticulum, colpoid streaks and semicircular, sexinous patches around the aperture; 2, 3, the same under different foci; 4, optical section.

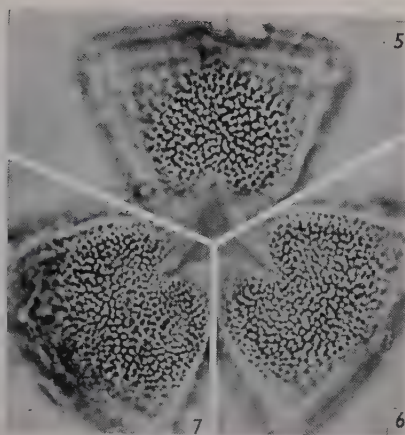
Plate 29. Figs. 1-7. *Sclerochiton boivini* (Baill.) C. B. Clarke ($\times 1000$; reduced from $\times 1500$). — 1, showing punctitegillate condition; 2, 5-7, infrategillar bacula bright; 3, bacula under lower focus; 4, optical section. Figs. 8-11. *Stenandrium trinerve* Nees ($\times 1000$; reduced from $\times 1500$). — 8, verrucae and other suprattegillar processes; 9, 10, the same under lower foci; 11, optical section. Figs. 12-14. *Sympagis brunoniana* (Nees) Brem. ($\times 1300$; reduced from $\times 2000$). — 12, narrow, wavy ridges; ridges joined in pairs in the apocolpium; areas outside the ridges usually spaced with small processes; 13, the same under lower focus; 14, optical section. — The "palynogram", Figs. 12-13, has been turned clock-wise about 30°).



1

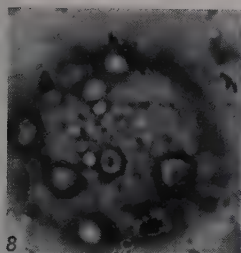


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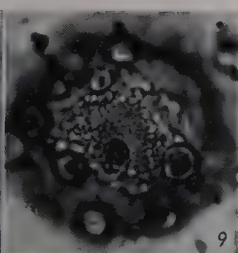


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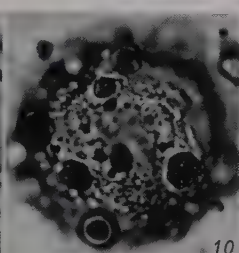
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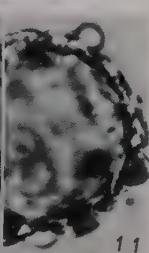
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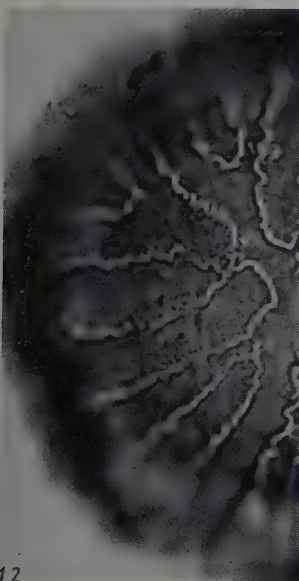
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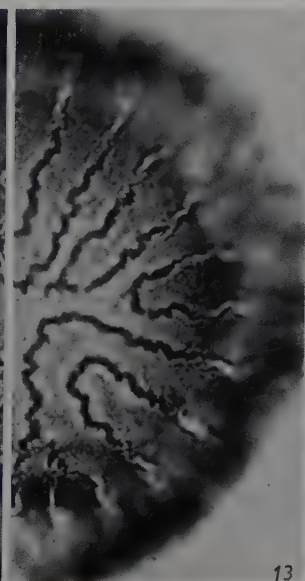
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11

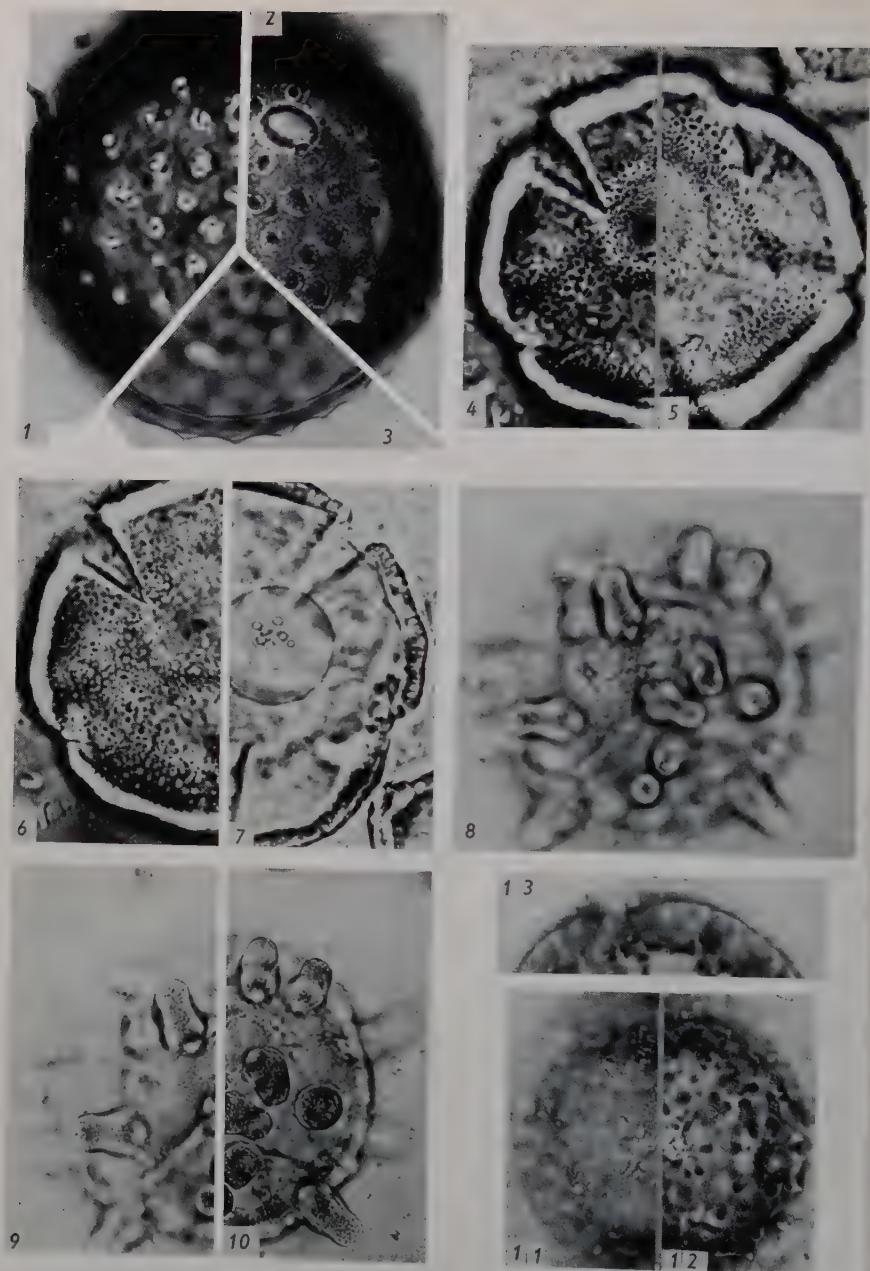


Plate 30. Figs. 1-3. *Styasasia* sp. ($\times 1000$; reduced from $\times 1500$). — 1, spinules (bright); 2, circular pore; spinules at a lower focus (dark); 3, optical section. Figs. 4-7. *Thomandersia laurifolia* (Benth.) Baill. ($\times 1000$; reduced from $\times 1500$). — 4-6, LO-pattern (see text, p. 46); 7, optical section. Figs. 8-10. *Thunbergia fragrans* Roxb. ($\times 750$; reduced from $\times 1500$). — 8, suprategillar, blunt processes; 9, 10, same under lower foci showing their spongy interior. Figs. 11-13. *Whitfieldia longifolia* T. Anders. ($\times 500$; reduced from $\times 1500$). — 11, spinules at high focus; 12, same under lower focus; small, infrategillar bacula are also shown; 13, optical section.

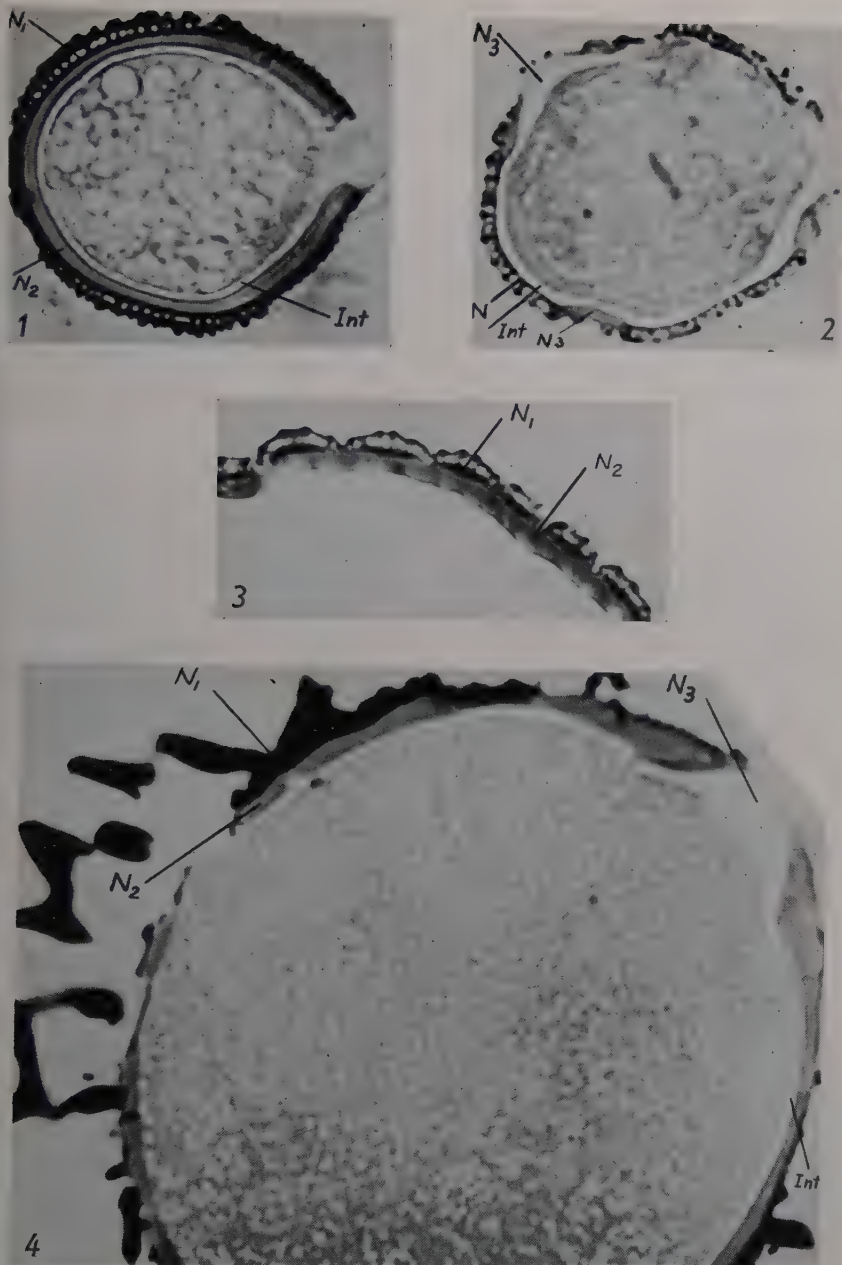


Plate 31. Fig. 1. *Adhatoda vasica*. — Fig. 2. *Andrographis paniculata*. — Fig. 3. *Asteracantha longifolia*. — Fig. 4. *Barleria prionitis*. — All $\times 1500$. Figs. 1, 2, 4: section through fresh pollen grains preserved in glacial acetic acid; fig. 3: section through an acetolyzed pollen grain. Abbreviations (used in plates 31–38): T=tegillum, T.L.=transparent layer, N=nexine, N1=nexine 1, N2=nexine 2, N3=nexine 3, Int.=intine.

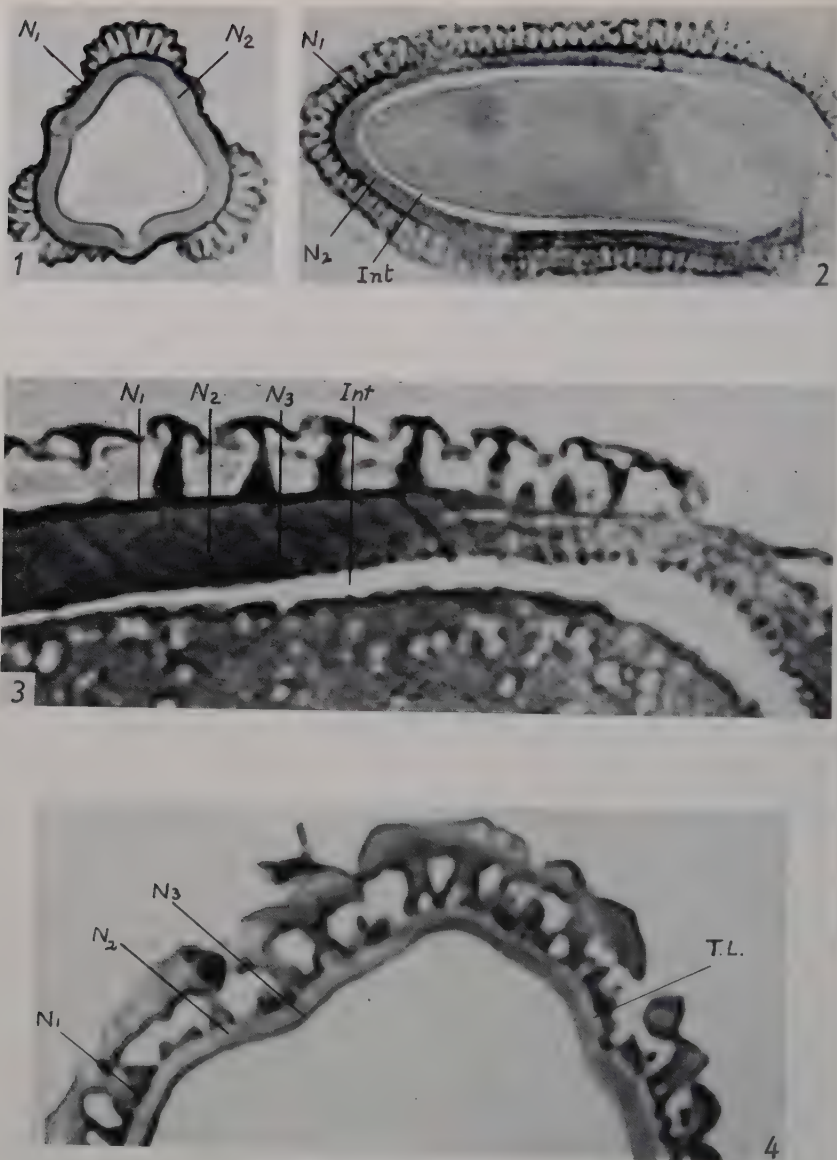


Plate 32. Fig. 1. *Drejerella guttata* ($\times 1000$). Fig. 2. *Blepharis boerhaviaefolia* ($\times 1500$). — Fig. 3. *B. molluginifolia*, UV micrograph (mercury low pressure lamp, 2750 Å), (7×1000). — Fig. 4. *Bravaisia floribunda*, section through an acetolyzed grain ($\times 1500$). — Figs. 1–3, sections through fresh pollen grains (preserved in glacial acetic acid).

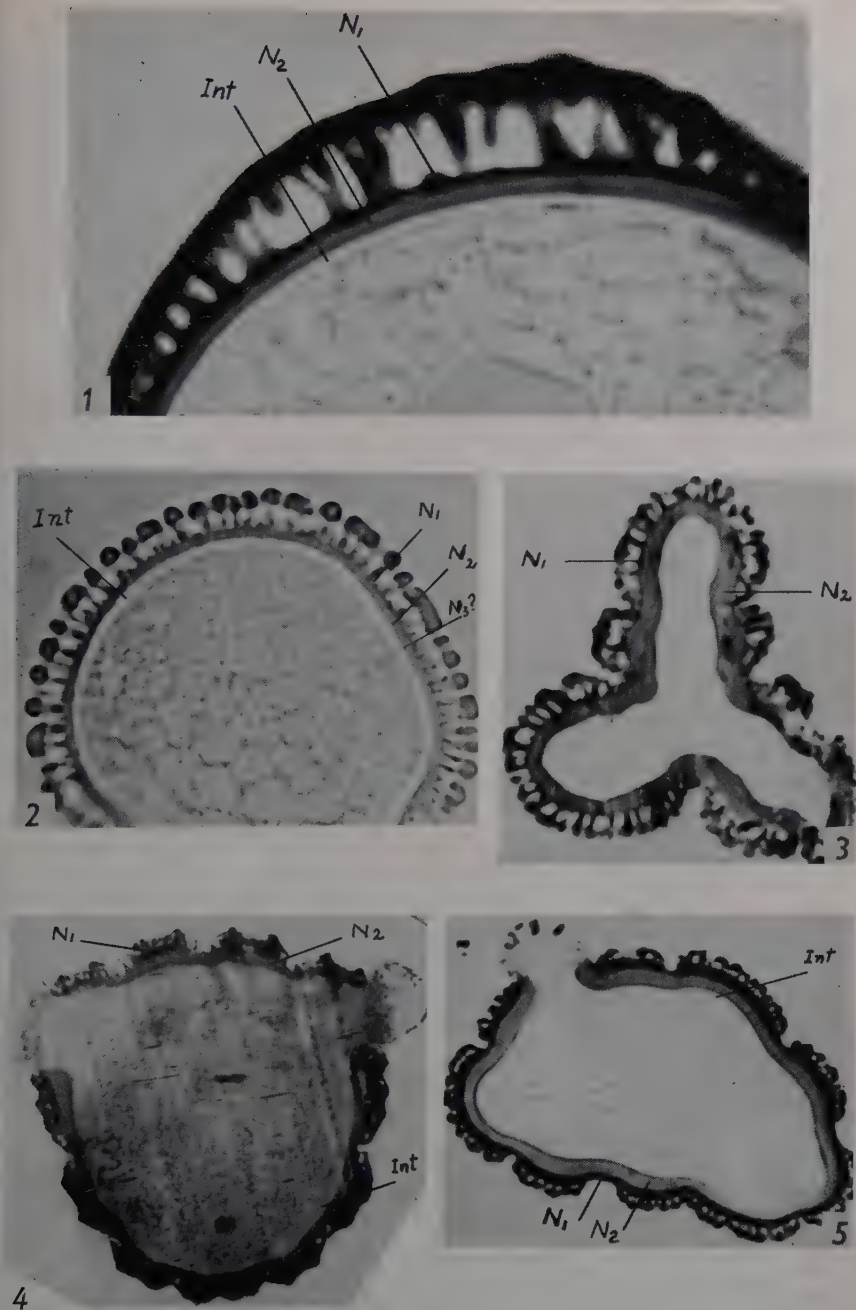


Plate 33. Fig. 1. *Jacobinia carnea* ($\times 3000$). — Fig. 2. *Pseuderanthemum carruthersii* ($\times 1500$). — Fig. 3. *Graptophyllum pictum* ($\times 750$). — Fig. 4. *Hygrophila angustifolia* ($\times 1500$). — Fig. 5. *Jacobinia coccinea* ($\times 1500$). — Figs. 1, 2, 4, 5, section through fresh pollen grains preserved in glacial acetic acid; fig. 3, section through an acetolyzed grain.

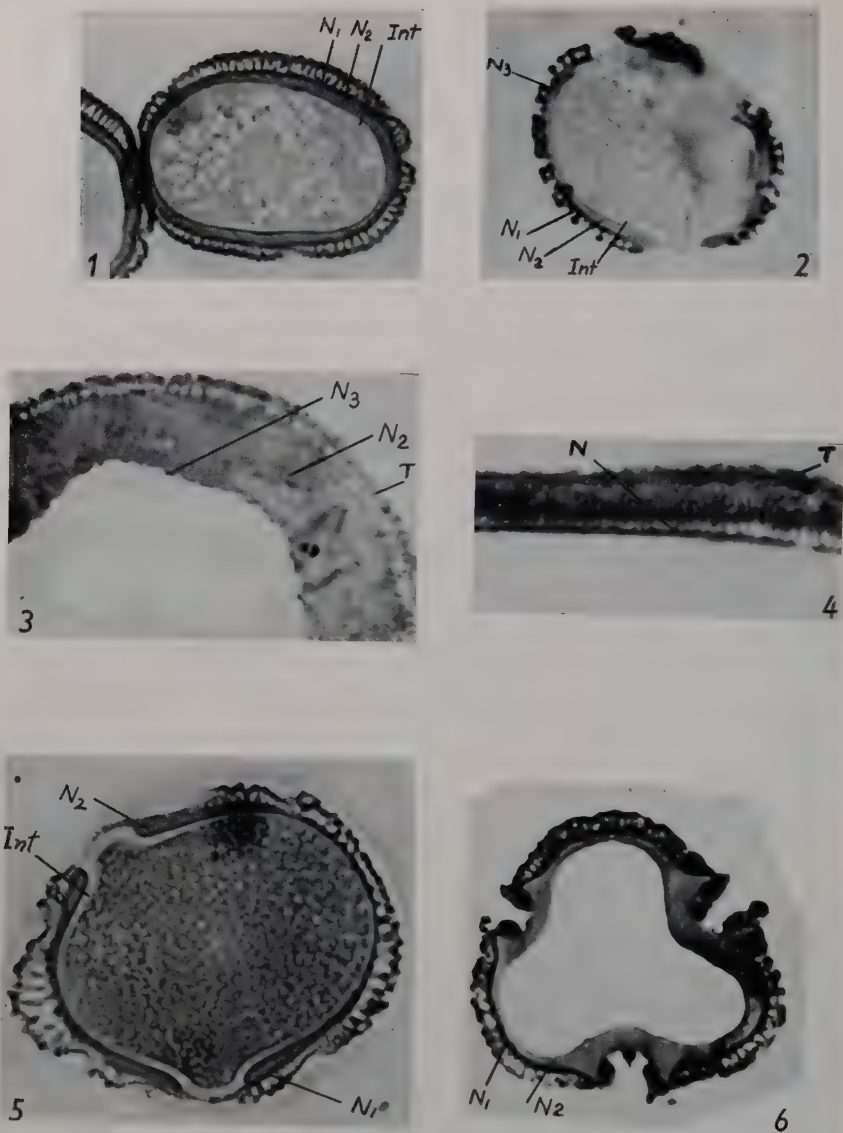
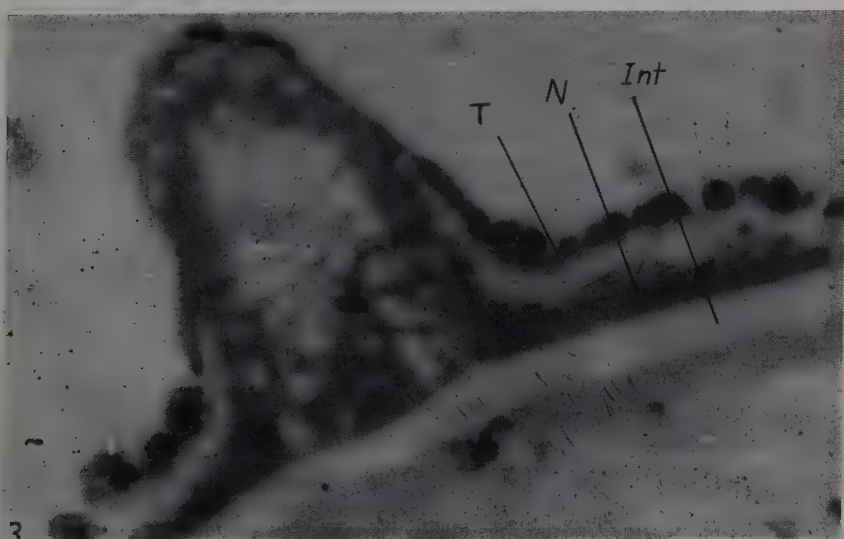
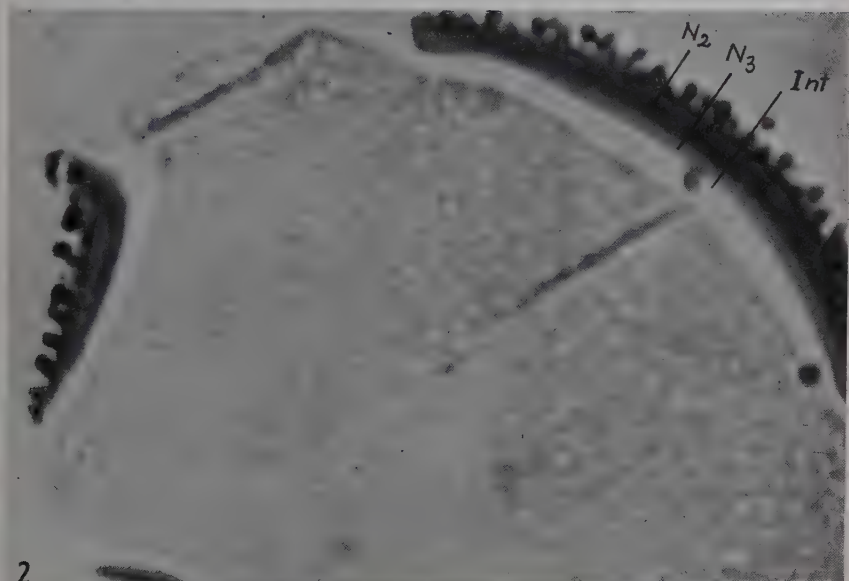
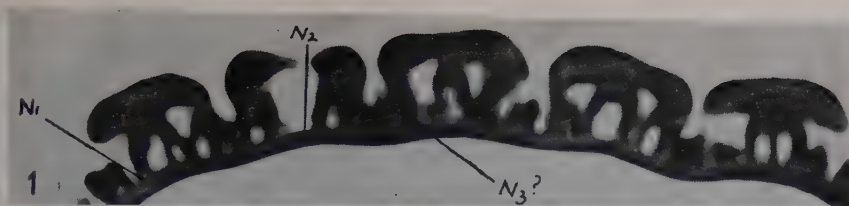


Plate 34. Fig. 1. *Justicia betonica* ($\times 1500$). — Fig. 2. *Lepidagathis cristata* ($\times 1500$). — Fig. 3. *Mendoncia costaricana* ($\times 1500$). — Fig. 4. *Meyenia hawtayneana* ($\times 1500$). — Fig. 5. *Peristrophe bicalyculata* ($\times 1500$). — Fig. 6. *Phlogacanthus curviflorus* ($\times 1500$). — Figs. 1, 2, 5, sections through fresh pollen grains preserved in glacial acetic acid; figs. 3, 4, 6, sections through acetolyzed grains.

Plate 35. Fig. 1. *Sanchezia klugii* ($\times 3000$). — Fig. 2. *Sesamum indicum* ($\times 1500$). — Fig. 3. *Thunbergia fragrans*, UV micrograph; mercury low pressure lamp 2536 Å (4.3×1100). — Fig. 1, section through an acetolyzed grain; figs. 2, 3, section through fresh pollen grains preserved in glacial acetic acid.



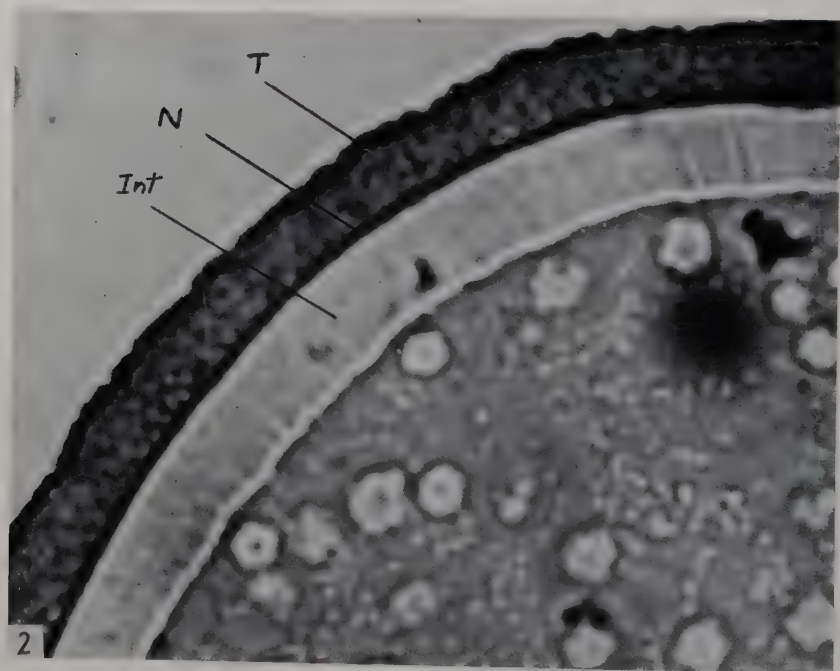
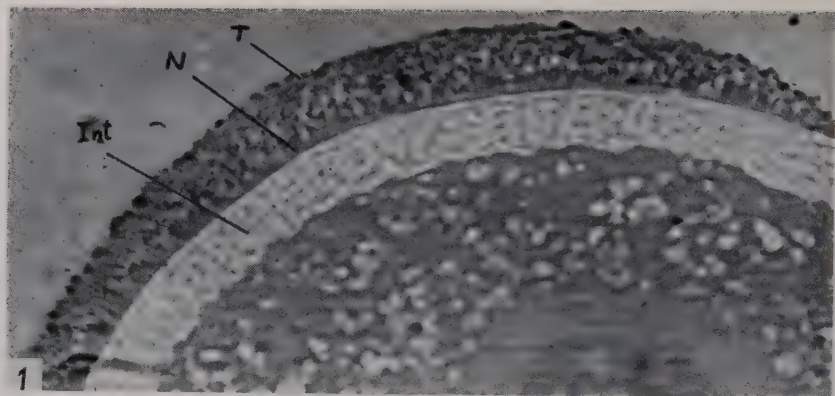


Plate 36. *Thunbergia grandiflora* (section through fresh pollen grains preserved in glacial acetic acid). — Fig. 1, UV micrograph; mercury low pressure lamp 2536 Å (2.5×1000). — Fig. 2, ordinary photomicrograph (3×1000).

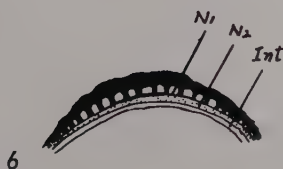
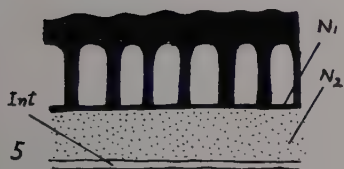
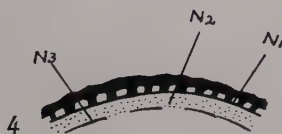
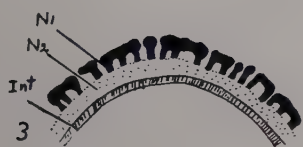
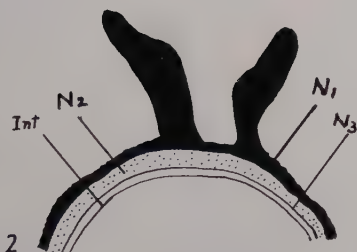
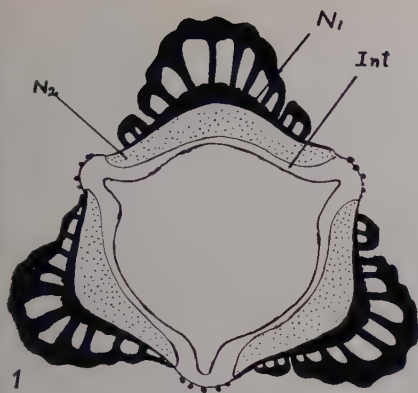


Plate 37. Fig. 1. *Asystasia coromandeliana*. — Fig. 2. *Barleria cristata*. — Fig. 3. *Crossandra undulataefolia*. — Fig. 4. *Ecbolium oreadam* (section through an acetolyzed grain). — Fig. 5. *Justicia gendarussa*. — Fig. 6. *J. platycarpa*. — All except Fig. 4 are sections through fresh pollen grains preserved in glacial acetic acid. — $\times 1000$ except Fig. 5 ($\times 4000$). — Sexine and nexine 1 black; rest of nexine dotted.

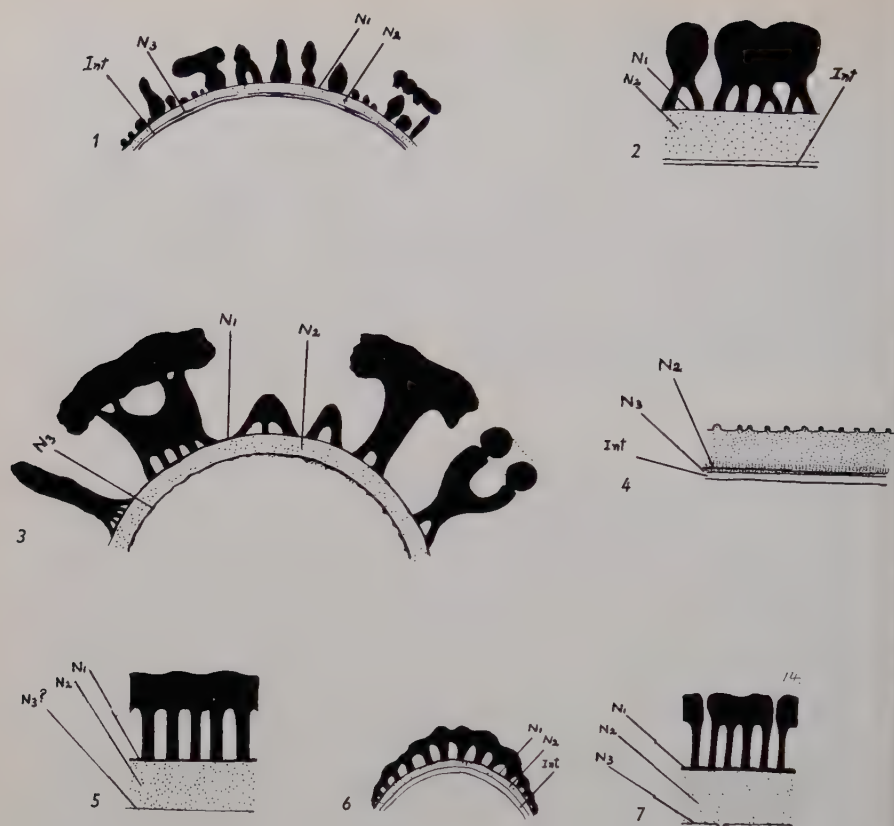


Plate 38. Fig. 1. *Ruellia formosa*. — Fig. 2. *R. speciosa*. — Fig. 3. *R. tessmannii*. — Fig. 4. *Sesamum latifolium*. — Fig. 5. *Spathacanthus hoffmanni*. — Fig. 6. *Stenandrium dulce*. — Fig. 7. *Strobilanthes alatus*. Figs. 1, 2, 4, 6, sections through fresh pollen grains preserved in glacial acetic acid. Figs. 3, 5, 7, sections through acetolyzed grains. — Sexine and nexine 1 full black; rest of nexine dotted. Approximate magnification: Figs. 1, 4, 6 $\times 2000$; Figs. 2, 7 $\times 3000$; Fig. 3 $\times 1000$; Fig. 5 $\times 3500$.

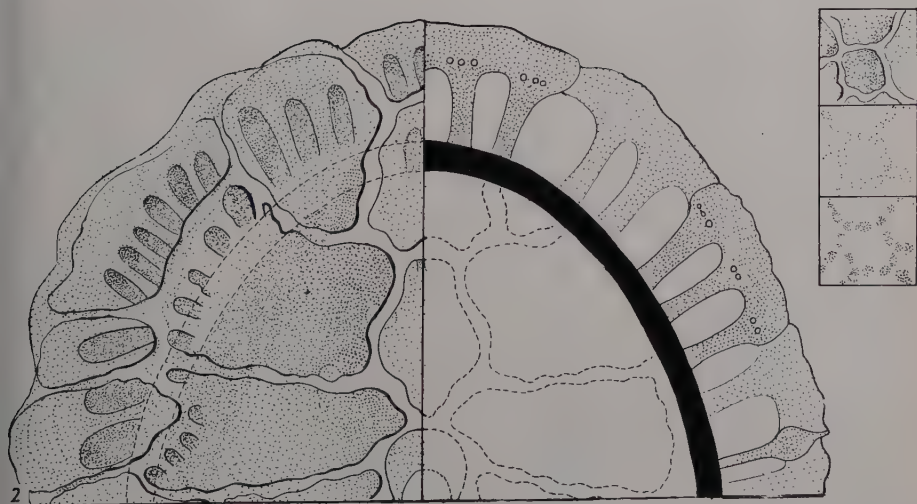
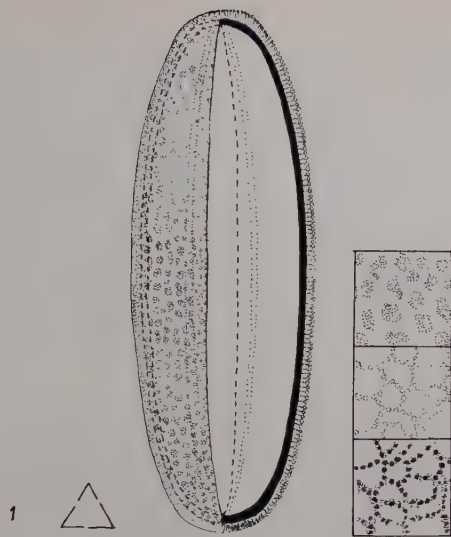


Plate 39. Fig. 1. *Aphelandra lyrata*. — Fig. 2. *Barleria courtallica*. — Sexine in Pl. 39–41 dotted; nexine full black. $\times 1000$.

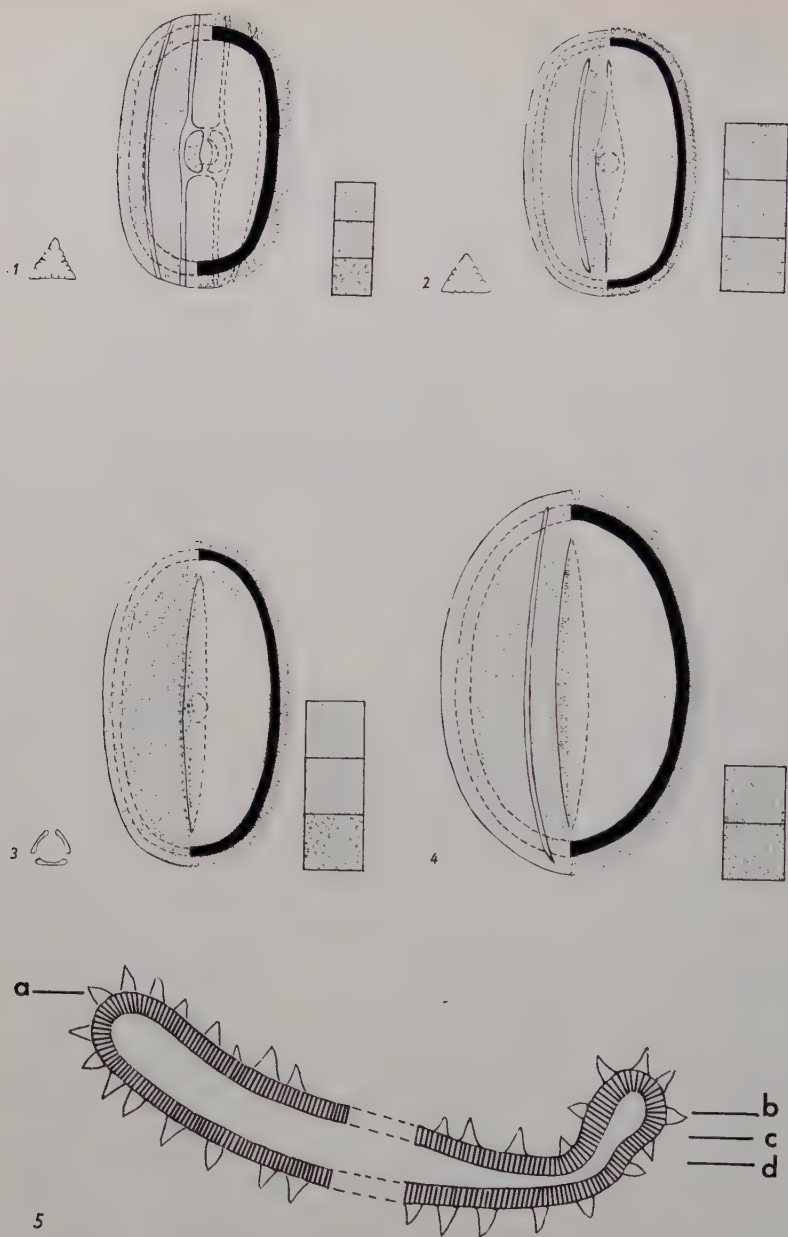


Plate 40. Fig. 1. *Phayloopsis longifolia*. — Fig. 2. *Carlwrightia californica*. — Fig. 3. *Phlogacanthus curviflorus*. — Fig. 4. *Haselhoffia nematosiphon*. — All $\times 800$ (reduced from $\times 1600$). — Fig. 5. *Kalbregerella rostellata*, diagram showing different foci (a-d) in Pl. 17, Figs. 1-4 respectively.

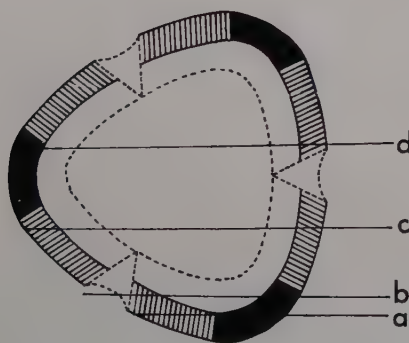
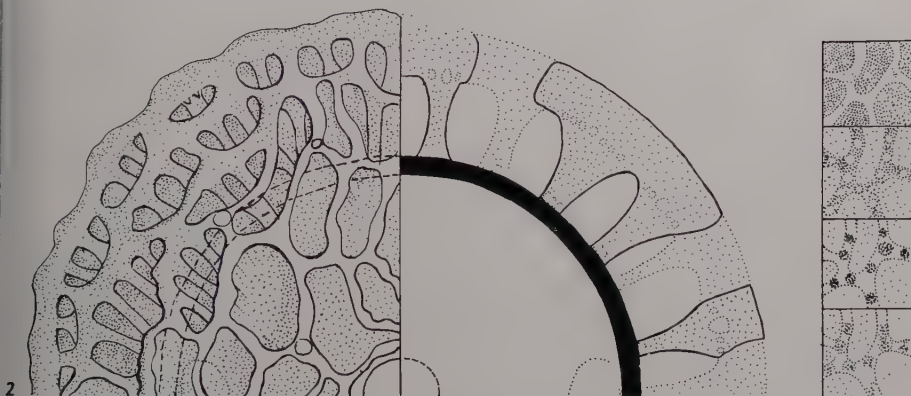
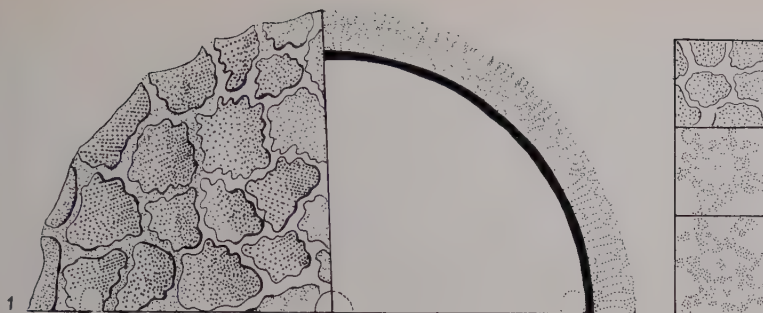


Plate 41. Fig. 1. *Ruellia amoena*. — Fig. 2. *R. tessmannii*. — Both $\times 1000$ (reduced from $\times 1600$). — Fig. 3. *Hulemacanthus whitei*, diagram showing different foci (a-d) in Pl. 14, Figs. 1-4 respectively.

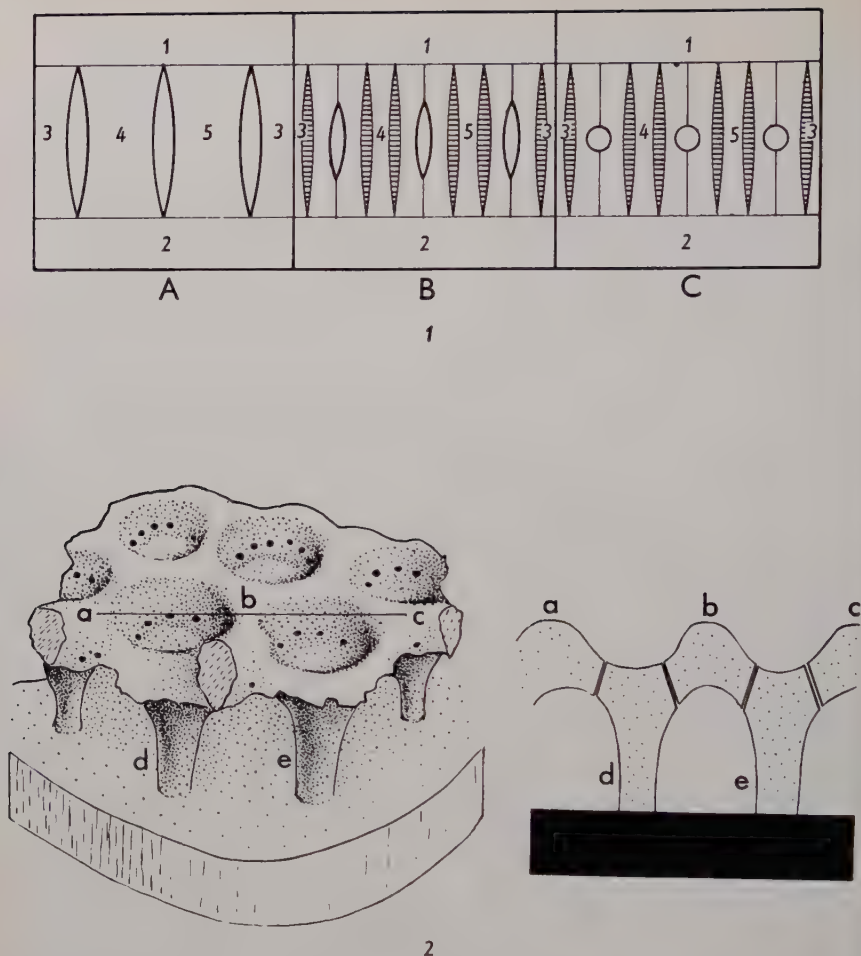
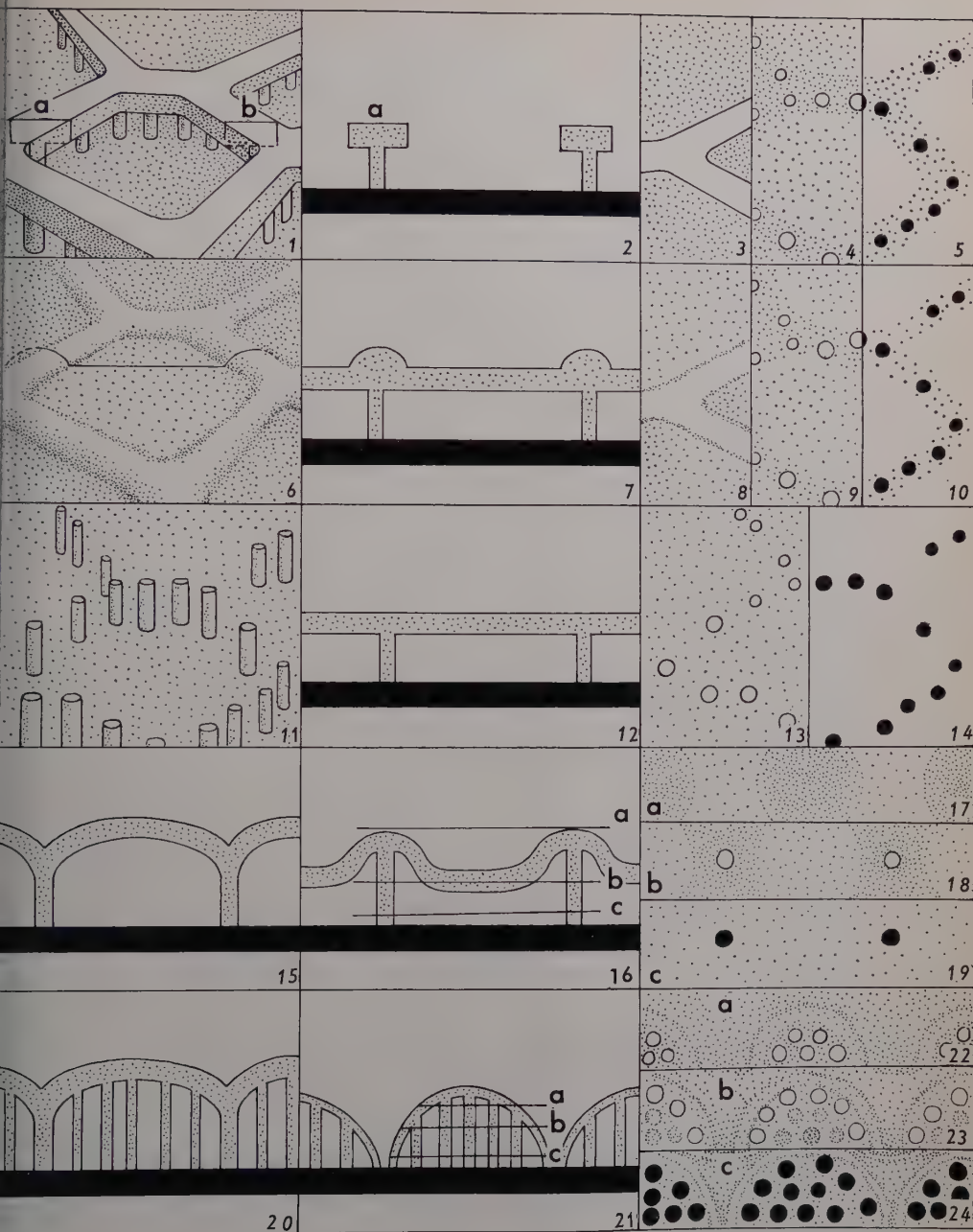

























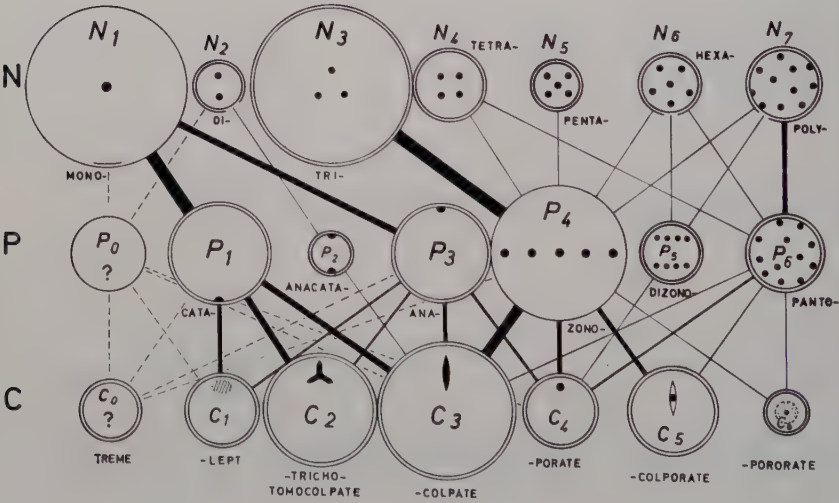
Plate 42. Fig. 1. Diagrammatic representation of the subdivisions of the surface of pollen grains with 3 colpi (A), 3 colpi and 6 colpoid streaks (B) and 3 pores and 6 colpoid streaks (C). — 1, 2, apocolpia; 3-5, mesocolpia. The thin, vertical lines in B and C mark, together with the aperture margins, the limit between each individual "mesocolpium". Colpoid streaks shaded. The mesocolpia in A are mesocolpia in the strict sense of the word. The "mesocolpia" in B and C are "mesocolpia" in a different sense, particularly in C, where there are pores instead of colpi. On account of the presence of colpoid streaks, the term mesocolpium has, however, been used in the present paper in the way shown above. — Fig. 2. *Hypoestes antennifera*. Diagram showing funnel-shaped bacula (the upper part of which amalgamate and form a tegillum); puncta, etc. as well as a section along the line a-c in the left figure.



(For explanation, see page after Pl. 44.)

ATRE- ME	N O M O T R E M E							ANOMO- TREME
<i>N</i> 0	<i>N</i> 1	<i>N</i> 2	<i>N</i> 3	<i>N</i> 4	<i>N</i> 5	<i>N</i> 6	<i>N</i> 7	<i>N</i> 8
								
	MONO-	Di-	IRI-	TETRA-	PENTA-	HEXA-	POLY-	
<i>P</i> 0	<i>P</i> 1	<i>P</i> 2	<i>P</i> 3	<i>P</i> 4	<i>P</i> 5	<i>P</i> 6		
								
	CATA-	ANACATA-	ANA-	ZONO-	DIZONO-	PANTO-		
<i>C</i> 0	<i>C</i> 1	<i>C</i> 2	<i>C</i> 3	<i>C</i> 4	<i>C</i> 5	<i>C</i> 6		
								
-TREME	-LEPT	-TRICHO- TOMO- COLPATE	-COLPATE	-PORATE	-COLP- ORATE	-POR- ORATE		

1



2

(For explanation, see next page.)

Plate 43. Diagrammatic representation of certain sexine patterns, some of which occur in the Acanthaceae.

Figs. 1-5. Reticulate ("eu-reticulate") pattern. 1, lumina and simplibaculate muri; 2, vertical section; 3-5, successive LO-patterns. — Figs. 6-10. Diagrams showing exine with supra- and infrategillar, reticulate patterns. 6, tegillum with luminoid areas surrounded by muroid ridges; 7, vertical section; 8-10, successive LO-patterns (9 and 10 showing an infrareticulate pattern). — Figs. 11-14. Diagram showing exine with infrategillar, reticulate pattern. 11, surface of nexine with endosexinous bacula arranged in a reticulate pattern (tegillum not shown); 12, vertical section; 13, 14, successive LO-patterns. — Fig. 15. Diagram (vertical section) of tectate exine with upper surface of tegillum slightly convex between supporting bacula. — Fig. 16. Same as Fig. 15 but with upper surface of tegillum slightly concave between supporting bacula. — Figs. 17-19. Successive LO-patterns of Fig. 16. — Figs. 20, 21. Hypothetical transition from a tectate (Fig. 20) to an insulate (Fig. 21) sexine. — Figs. 22-24. Successive LO-patterns corresponding to levels a, b, c in Fig. 21.

Plate 44. Figs. 1, 2. NPC-classification (diagrammatic representation; cf. also Erdtman and Straka 1961).

The classification is based on the apertures, their number (N), position (P) and character (C). There are nine N-classes (N 0-8), seven P (P 0-6) and seven C classes (C 0-6). N 0: atreme spores (spores without aperture); P 0: spores where the position of the aperture(s) is not known; C 0: spores where the character (shape etc.) of the aperture(s) is not known.

The circles N1 and N3 in Fig. 2 are larger than the rest and thereby emphasize that mono- and tritreme spores are more common than di-, tetra, pentatreme etc. The size of the P- and C-circles is likewise approximately proportionate to the frequency of the features in question and so is also the thickness of the lines interconnecting the circles. Broken lines connote that the position or the character (or both) of the aperture(s) is not known. Single circles signify that the name of the feature in question is usually omitted. Example: a "tri-zonoporate" grain (classification number N3-P4-C3, or simply 343) is referred to as "triporate", not as "trizonoporate" (P4 is surrounded by a single circle, N3 and C3 by a double circle). "100" is a monotreme, 111 a catalept, 764 a polypantoporate and 654 a dizonoporate (3+3) spore. (Diagrams reproduced by courtesy of Prof. Gunnar Erdtman.)

POLLEN MORPHOLOGY AND SPORODERM STRATIFICATION IN *LINUM*

BY

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In a description of the exine stratification in *Linum*, Erdtman (1952) mentioned two alternative interpretations. According to the first alternative the nexine is very thin and the overlying process-bearing sexine relatively thick. According to the second alternative the nexine is the main layer, the sexine being restricted to the processes. The difficulty of drawing a demarcation line between sexine and nexine is due to some of the endomorphic features of the exine.

A UVMG of *Linum angustifolium* (Pl. VI, Fig. 2 in Erdtman 1959), shows three exine layers, two of which are more or less solid, encompassing a layer irregularly interlaced by more or less baculoid rods. Similar features are shown in an EMG of *Linum adenophyllum* by Barbro Afzelius (1956, Fig. 10, p. 33).

The present study is a more detailed investigation of the sporoderm stratification in *Linum*. Fortyfour species were studied. Fresh material of *Linum perenne* and *L. angustifolium* was obtained from plants grown at the Hortus Bergianus, Stockholm. Material of *Linum austriacum*, *L. bienne*, *L. bulgaricum*, *L. extraaxillare*, *L. tenuifolium* and *L. usitatissimum* was collected from plants grown at the Botanical garden of Uppsala, while fresh material of *Linum alpinum* and *L. hologynum* was obtained from the Botanic garden, Edinburgh (coll. Sivert Nilsson, Stockholm). The other material came from herbarium specimens (Tab. 1).

Polliniferous material from fresh plants or herbarium specimens was suspended in glacial acetic acid and then acetolyzed *lege artis*

(cf. Erdtman, Svensk bot. Tidskr., Vol. 54, pp. 561–564, 1960). A part of this material was chlorinated after acetolysis. The grains were embedded in glycerine jelly. Another part of the polliniferous material was only chlorinated (not acetolyzed) and stained with an aqueous solution of ruthenium red. This technique was found to be particularly helpful in the study of the sporoderm stratification (cf. also Bailey 1960 and others). The intine is distinctly and rapidly stained both in fresh pollen grains and in pollen grains from herbarium specimens. The exine, on the contrary, does not take the stain.

For thin sectioning pollen grains from fresh plants or herbarium specimens were fixed in glacial acetic acid, dehydrated and embedded in methacrylate (Erdtman 1957). It was, however, observed that pollen grains in herbarium specimens up to 65 years old were well preserved. Thin sections through their walls were quite as good as those made from fresh material, sometimes even better.

Gross Morphology

Shape

The pollen grains are either spheroidal, prolate spheroidal, or subprolate (Tab. 1). Amb more or less circular.

Size

The length of the polar axis varies in subprolate grains from 40 μ in *L. micranthum* to 80 μ in *L. hologynum* and *L. lewisii* (Tab. 1). Spheroidal grains have particularly large diameters (in *L. heterospalum*, *L. multicaule* and *L. rigidum* 75, 100 and 125 μ respectively).

Apertures

The grains are 3-colpate, pantocolpate or pantoporate.

Out of the 44 species studied, 37 have tricolpate grains. Most of them have their colpi in the form of narrow elongated streaks equally spaced around the equator. The colpi are covered with a thin membrane, provided with the same kind of processes as found in the meso- and apocolpia. The colpi are easily seen in grains in polar view. In equatorial view, however, they are not always easily discernible on examination of the surface, especially in non-transparent grains. Colpi of this kind are found in many species, e.g., *L. hirsutum* (Pl. 1, Figs. 3, 4) and *L. catharticum* (cf. Tab. 1). In *L. austriacum*, *L. perenne* and *L. bienne*, the colpus is broader, ap-

pearing as an elongated oval or dumbell-shaped area in the exine (Pl. I, Fig. 1). In *L. alpinum* and *L. betseliense* a short longitudinal slit appears in the centre of the colpus membrane (Pl. II, Fig. 2). In the remaining species, e.g., *L. bulgaricum*, *L. flavum* and *L. grandiflorum*, the colpus consists of a longitudinal slit or groove in the sexine (Pl. I, Fig. 5). In this type the colpus is covered with a very thin nexine layer, sometimes carrying small verrucoid processes. The colpus slit is surrounded by sexinous processes bent sideways towards the colpus parallel to the surface of the grain (Pl. I, Fig. 6). During germination or expansion of the grain no rupturing of the sexine takes place. In polar view an expanded grain shows such a slit widely open (Pl. I, Fig. 6), with a more or less straight outline. In *L. austriacum* and *L. hirsutum* the borders of the colpi have a wavy, ruptured appearance (Pl. I, Figs. 2 and 4).

Thus in the tricolpate pollen grains four types of colpi can be recognized (Plates I, II). 1. Broad covered colpus with a short slit (example: *L. alpinum*). — 2. Broad covered colpus (example: *L. austriacum*). — 3. Narrow elongated covered colpus (example: *L. hologynum*). — 4. Narrow elongated uncovered colpus with slit (example: *L. flavum*).

Pantocolpate dodecatreme grains were found only in *L. monogynum* and *L. jamaicense*. The colpi are so arranged that their axes converge towards eight triradiate centres dividing the surface of the grain into six squares. If the grain is examined with one of these centres exactly uppermost (Pl. II, Fig. 6), focusing downwards will bring into view another center exactly below but with its radii alternating with those of the above center. "If the grain is oriented so that the axes of the colpi on the upper surface form a square, focusing down will bring into view another square exactly subtending the one above and four other colpi will be seen bending over the limb from the angles of one square towards the corresponding angles of the other square" (Wodehouse 1935). The grains in *L. monogynum* (Pl. II, Figs. 4–7) have relatively thicker sexine than *L. jamaicense* ($1.5\ \mu$). The apertures in *L. jamaicense* are irregular in outline (often more poroid than colpoid).

Pantoporate grains were found in *L. heterosepalum*, *L. multicaule*, *L. olgae*, *L. rigidum*, and *L. stelleroides*. The pores in these species are covered with the same pattern of processes as the non-porate regions. In *L. rigidum* (Pl. III, Figs. 1–2) and *L. multicaule* (Pl. III, Figs. 3, 4) the sexine is very thick (10 and $6\ \mu$ respectively). The

sexine in the other porate grains, e.g. *L. heterosepalum*, *L. olgae* and *L. stelleroides* (Plate III, Figs. 5, 6), is relatively thin and the pores are filled with processes, the length of which is nearly the same as the thickness of the exine. The pores are, therefore, difficult to detect (cf. also Pl. VII, Fig. 5).

The pores in all these species can be detected by careful LO-analyses of the exine, as the lowest focus shows the pore processes as a number of minute circles representing their free roots, while the non-apertural processes lack such roots. Careful examination of thin sections reveals that the pores have a thin nexine membrane, in which the free processes are rooted (cf. e.g. Pl. III, Fig. 2).

Such a pore could be described as a "cryptopore" in analogy with the cryptocolpi (Erdtman 1952) in the colpate species of *Linum*. The pollen grains in *L. rigidum* and *L. multicaule* are "hemicyptoporate" if compared with the true cryptoporate grains in *L. stelleroides* and *L. olgae*.

Sporoderm Stratification

As mentioned before, there are two alternative interpretations of the stratification of the exine in *Linum*: either is the nexine very thin and the sexine very thick, or does the sexine only include the free exinous processes. For reasons mentioned below the first alternative seems to be correct.

The pollen wall in *Linum* exhibits three layers: 1, exine, comprising sexine and nexine; 2, an intermediate layer, probably "medine", between the exine and intine in colpate grains; 3, intine.

Sexine

The sexine is differentiated into three layers. To avoid confusion with the numerous terms put forward by different authors they are termed S_1 , S_2 , and S_3 starting from outside. Sexine 1 (S_1) consists of the processes emerging from the main layer of the sexine (S_2). They differ greatly in shape, height and size (cf. Fig. 1). Some are small, usually conical, sharply pointed (Fig. 1: 1-3). In cross section they are all rounded, sometimes more or less polygonal at their bases. In *L. alpinum* and *L. grandiflorum* they are cylindrical with a number of spinuloid excrescences at the top (Fig. 1: 4). In *L. angustifolium* and *L. austriacum* they are verrucoid (Fig. 1: 5), in *L. olympicum* and *L. olgae* gemmoid (Fig. 1: 6), in *L. bulgaricum* and *L. flavum* piloid (Fig. 1: 7). In the porate grains of *L. multicaule*,

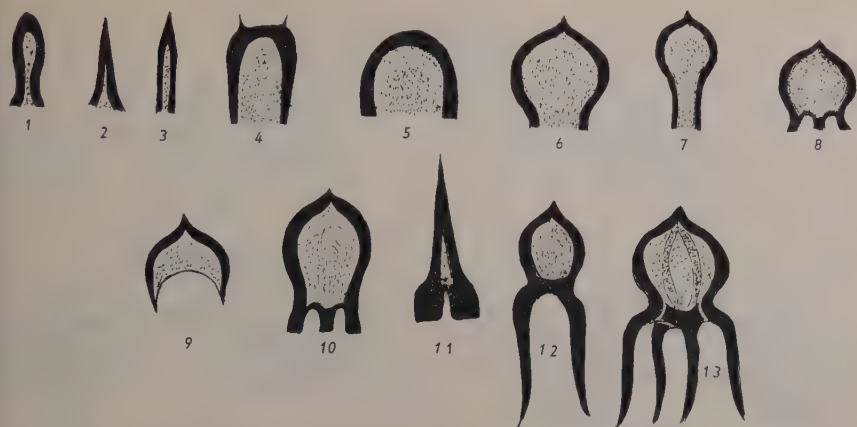


Fig. 1. Processes in *Linum* pollen. — 1-3, *L. bulgaricum* and *L. grandiflorum* (small processes). — 4, *L. grandiflorum* (cylindrical processes). — 5, *L. austriacum* (verrucoid processes). — 6, *L. olympicum* (gemmoid processes). — 7, *L. bulgaricum* (piloid processes). — 8, 12, 13, *L. rigidum* ("bacularia"). — 9, *L. perenne* (pore process). — 10, *L. heterosepalum*. — 11, *L. olgae* (small process; large processes gemmoid).

L. heterosepalum, and *L. rigidum* the large processes have short free baculoid roots at their bases (Fig. 1: 8). In such grains the processes covering the pores have long free roots (the small ones usually have two roots, while the big have a variable number of baculoid roots; cf. Fig. 1: 12-13). In *L. perenne* very short roots were noticed at the base of the processes covering the colpi (Fig. 1: 9).

The large processes are, as also shown by LO-analyses, formed by closely packed more or less amalgamated small processes. The degree of amalgamation varies in different species. The individual units amalgamated to form the bigger processes can be traced as a number of small bright dots at the top of the processes in the uppermost focus in *L. heterosepalum* and *L. thunbergii* (Fig. 3 B: 1, p. 115). In *L. grandiflorum* (Pl. IV: 1), *L. austriacum* and others these units can be seen at a lower focus while in other species, e.g. *L. mumbyanum* and *L. olympicum*, they can be seen along the whole length of the processes (Fig. 3 A: 1-5). In some species, e.g. *L. bulgaricum* and *L. multicaule* (Fig. 4 e, p. 127), the amalgamation is complete, i.e., no individual elements can be seen.

In all big processes the components are arranged in a circle like iron bars in a concrete pillar. They seem to be cemented together by some hyaline material which differs from that in the central part. The latter is generally granular and continuous with the sexinous material

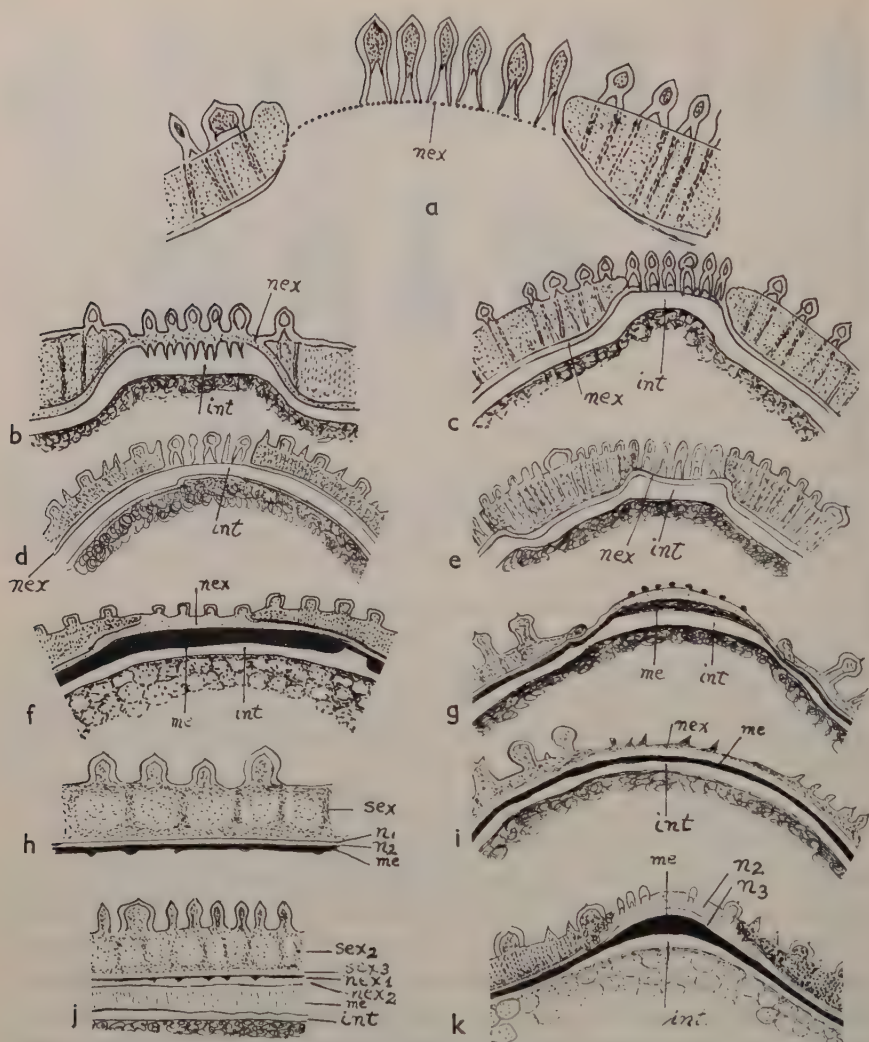


Fig. 2. Diagrammatic representation of sporoderm sections. — a, *Linum multicaule*. — b, c, *L. rigidum*. — d, *L. stelleroide*s. — e, *L. multicaule*. — f, *L. angustifolium*. — g-h, *L. bulgaricum*. — i-j, *L. grandiflorum*. — k, *L. perenne*. — a, acetolyzed, b-k, not acetolyzed material. — int, intine; me, "medine"; nex, nexine; sex, sexine.

underneath. In some species, e.g. *L. grandiflorum*, the processes as well as the sexine surface, from which they rise, are covered with a definite layer of different character, perhaps "stegine" (provisional term suggested by Erdtman). It is nongranular-amorphous like the medine layer.

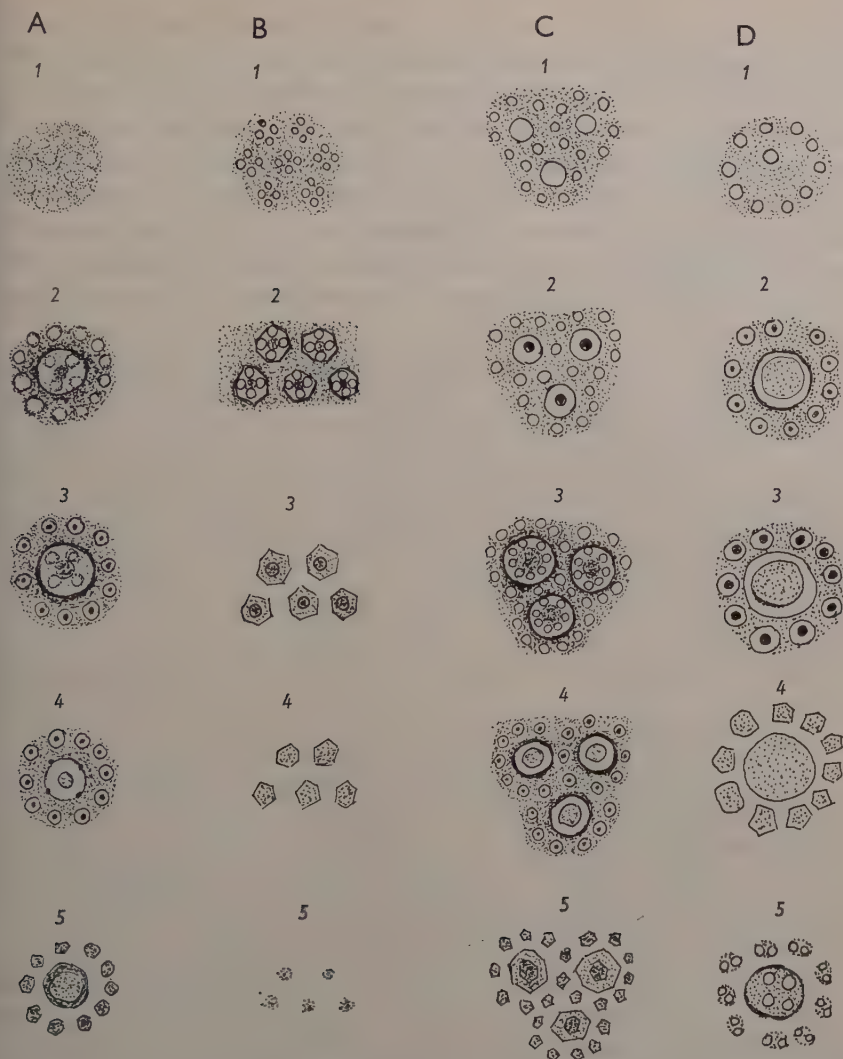


Fig. 3. — Lo-analyses. — A, *Linum mumbyanum*. — B, *L. thunbergii*. — C, *L. austriacum*. — D, *L. olgae*.

The processes rising from the general sexine surface are either monomorphic (Plate IV: 5–7), dimorphic (Pl. IV: 1–3), or heteromorphic, i.e., of variable size (Pl. IV: 8). The pollen grains in fresh material of *L. flavum* (all flowers were short-styled) and brevistylous flowers of *L. perenne* and *L. austriacum* have monomorphic processes. *Linum catharticum*, *L. adenophyllum*, *L. californicum* and *L. breweri*

are known to have homostylous flowers, and their pollen grains were found to have monomorphic processes (Tab. 1). Fresh pollen grains from *L. bienne*, *L. tenuifolium* and *L. usitatissimum*, also known to be homostylous, had very small processes, the smallest in all *Linum* species, with a few relatively big processes interspersed among the small ones. Pollen grains from *L. bulgaricum* (all flowers longistylous) and longistylous flowers of *L. austriacum*, *L. grandiflorum* and *L. perenne* were found to have dimorphic processes. The pollen grains in *L. hirsutum*, *L. mumbyanum*, *L. strictum* and *L. viscosum* have heteromorphic processes (marked "> 2" in Tab. 1, p. 122).

The processes are sometimes very minute ($0.5\ \mu$ or less in diameter in *L. bienne*, *L. californicum*, *L. schiedeanum* and *L. usitatissimum*). The average diameter of the processes in the monomorphic grains is about $1.5\ \mu$ (Tab. 1), or larger ($2\ \mu$), as in *L. alpinum* and *L. hologynum*. In the dimorphic pollen grains the big processes have an average diameter of $2\ \mu$, e.g. in *L. bulgaricum* and *L. extraaxillare*, but they may also be larger (e.g. $3\ \mu$ in *L. grandiflorum*, *L. mumbyanum* and *L. perenne*). In the porate grains the diameter of the large processes may reach $3\text{--}4\ \mu$ (*L. heterosepalum*, *L. olgae*). The diameter of the small processes in the dimorphic species is usually about $1\ \mu$.

The variation in height of the processes is shown in Tab. 1. *Linum breweri*, *L. californicum*, *L. schiedeanum* and *L. usitatissimum* have the shortest processes ($0.5\text{--}1\ \mu$), *L. bulgaricum*, *L. mumbyanum*, and the species with porate pollen grains the longest ($3\text{--}4\ \mu$). In *L. breweri*, *L. californicum*, *L. micranthum* and *L. schiedeanum* (all American), the small processes are united, forming a tegillum.

Sexine 2 (S_2) forms the bulk of the exine. In *Linum extraaxillare*, *L. schiedeanum* and *L. tenuifolium* the thickness of this layer does not exceed $1\ \mu$. In other species it is generally about $2\text{--}3\ \mu$ thick, but it may also be much thicker, up to $6\ \mu$ in *L. multicaule* and $10\ \mu$ in *L. rigidum*. Usually this layer becomes thinner towards the apertures. In thin sections of *L. angustifolium*, *L. grandiflorum* and *L. perenne* (Fig. 2 f, i-k) this layer as well as the processes appear granular with no internal detail, but the granules are aggregated in certain parts, especially at the base and the periphery, leaving irregular spaces in the centre with less dense granulation. In thin sections of *L. flavum* and *L. bulgaricum* baculoid details could be seen in the granular matrix (Fig. 2 h and Pl. VI: d). In the porate grains, e.g. in *L. multicaule* and *L. rigidum*, thin sections showed well defined baculoid rods connected with the free roots of the superimposed

processes (Fig. 2 a and Pl. III: 2-3). These rods are still surrounded by granular matrix. In *L. catharticum* the sexine layer is formed of thick baculoid rods looking like teeth fixed in a jaw. In some sections these rods unite at the top forming a tegillum, surmounted by suprattegillar sexinous processes. No trace of granular tissue was seen between the bacula (Pl. VII: 4).

In some species (*Linum angustifolium* and *L. perenne*) thin sections as well as good ordinary pollen slides show a clear and distinct narrow non-granular S_3 -layer below the sexine 1 and 2 (cf. e.g. Fig. 2 j).

Nexine

The nexine forms a relatively thin layer below the sexine. In the nonapertural regions two layers could be differentiated, the outer a deeply stained very thin layer separating the sexine from the nexine. This layer ends at the aperture margins. It appears dark green in acetolyzed and un-acetolyzed grains treated with ruthenium red and fuchsin. In thin sections of *L. perenne* and *L. grandiflorum* very small projections are seen in this layer. They are directed inwards (cf. Fig. 2 j). Next to this layer is an inner, relatively thick, yellowish green, strongly refracting layer. In thin sections stained with fuchsin this layer usually has a very faint colour.

Thin sections of *Linum angustifolium*, *L. grandiflorum* and *L. perenne* show that the colpus membrane consists of two nexinous layers, an outer more or less granular layer, in which the sexinous processes are rooted, and an inner almost colourless layer. They are superimposed upon a darker, deeply coloured third layer which may represent the "intermediate" layer (the "medine"; cf. Pl. VI: a-c). In *L. bulgaricum* and *L. flavum* the colpus membrane is a very thin nexinous layer, sometimes provided with minute sexinous processes (Fig. 2 g).

In the porate grains the nexine is also relatively thin (cf. e.g. *Linum multicaule*, Fig. 2 a). It is differentiated into N_1 and N_2 . N_1 is absent from the pores. N_2 extends to form the pore membrane which carries the characteristic processes described above.

In acetolyzed grains of *Linum austriacum* and *L. extraaxillare* the nexine appears at the ruptured colpi as a bright refracting loop (Pl. II: 1, upper right colpus).

"Medine"

Non-acetolyzed entire grains (stained with fuchsin and ruthenium red) of species with colpate pollen grains showed, as well as thin sections stained with fuchsin, a relatively thick reddish layer

("medine") between the nexine and the intine. This layer easily takes the colour of both dyes. In non-acetolyzed chlorinated grains stained with fuchsin it swells and appears as opaque plugs in the colpi outside the colourless intine. In grains stained with ruthenium red it is coloured in much the same way as the intine, although less distinctly. In thin sections of non-acetolyzed grains of *Linum angustifolium* (Pl. VI: a-b), *L. grandiflorum* (Fig. 2 i, j) and *L. perenne* (Pl. VI: c) stained with fuchsin the layer appears as a thick opaque uneven layer interrupted by gaps or bearing projections directed towards the intine. It is thickened at the colpi where it appears as a dark-coloured layer outside the refracting intine and overlain by the bright or almost colourless nexine (Pl. VI: a).

In *Linum bulgaricum* and *L. flavum* this layer is much thinner than in the above species. It is thickened at the colpi, where it may be covered with a thin nexine layer, and underlain by a relatively thick layer of intine. In the porate grains it is unclear or even absent. Probably the "medine" does not resist acetolysis as it is usually absent in acetolyzed grains.

Intine

In un-acetolyzed grains stained with ruthenium red the intine usually appears as a thin refracting reddish layer. Probably only the outer part of the intine is stained (the colour disappears at lower focus). In thin sections of un-acetolyzed grains stained with fuchsin the intine appears as a thin colourless refracting layer tightly encircling the protoplasm and slightly thickened at the colpi. *L. flavum*, *L. bulgaricum* and the species with porate pollen grains are characterized by a more substantial intine.

Generally the intine is much thinner in the non-apertural than in the apertural regions. In thin sections it sometimes shows a faint lamellation. In optical sections of zonocolpate pollen grains in polar view it has, in contradistinction to the exine, a circular inner outline.

Cementing of layers

Sections through mature pollen grains of *Linum* demonstrate the cementing of the different layers of the pollen wall by wedge-shaped processes. Such processes extend from the outer part of the nexine into the inner part of the same. The latter is also provided with processes wedged into the medine or the intine particularly at the margins of the colpi. In *Linum bulgaricum* protoplasmic processes penetrate the intine proceeding as far as to the medine. There are no distinct processes of the latter kind in porate grains.

Discussion

The granular nature of the exine seems to represent a "primitive" state of structure which phylogenetically has led to the elaborate baculoid sexinous elements in more "advanced" species. (For the phylogenetic development of the exine, see Addendum, p. 126). The condensation of granular elements in the exine probably starts in the inner part leading to the formation of a solid non-granular nexine (the granular origin of the latter can be seen at the colpi where the nexine forms granular apertural membranes).

N_1 and N_2 have been traced by Afzelius in *Cedrus* (1956), Stix in the Compositae (1960), Bhoj Raj in the Acanthaceae (1961) and Saad in *Sonchus* and *Launaea* (1961), etc. Nexine 3, observed, i.a. by Erdtman (Erdtman and Praglowski 1959) in some proteaceous plants, could not be traced with certainty in *Linum*. However, thin sections seem to indicate that the colpus membranes consist of two layers (Fig. 2 k), viz. an outer granular and an inner non-granular layer, which latter may correspond to the endonexine, N_3 , of Erdtman. "Stegine", which like a thin varnish covers the sexine, has been encountered in various plants [cf. Afzelius 1955, Ehrlich 1958, Mühlethaler 1955, Rowley 1959, and Wettstein (Pl. V: d-e in Erdtman 1957)]. It has also been found in some *Linum* species. It does not resist acetolysis.

The intermediate layer ("medine") between the intine and the nexine in colpate *Linum* pollen grains has the following characters:

1. It does not resist acetolysis. — 2. It swells during chlorination and bulges at the colpi forming plug-like structures. — 3. It is easily stained with ruthenium red and basic alcoholic fuchsin, but it becomes opaque with ruthenium. — 4. In some species (*L. angustifolium* and *L. perenne*) it is much thicker than both nexine and intine. In other species it is thinner than the intine. It is usually thinner in the mesocolpia, thicker under the colpi (forming the main part of the colpus floor). — 5. The medine is often interrupted by small gaps. — 6. During sectioning rupturing often occurs between this layer and the intine. — 7. The medine sometimes shows a faint lamellation. It can be interpreted: a, as a special outer layer of the intine (exintine); b, as the innermost layer of the nexine, i.e. N_3 or endonexine; c, as an intermediate layer ("mesine" or medine; cf. Afzelius 1956, Ehrlich 1958, Rowley 1959) between the exine and the intine. As to the first suggestion, some authors, as Mühlethaler (1953), Sitte

(1953) and Bailey (1960; cf. also Wodehouse 1935), have shown that the intine consists of two layers, an inner relatively thin cellulosic layer and an outer non-cellulosic part which is rapidly and intensively stained in a dilute aqueous solution of ruthenium red. The outer layer is thickened at the apertures. They also found that the cellulose-containing inner layer of the intine has a relatively uniform thickness in contrast to the outer part of the intine. During disruption the cellulose layer of the intine commonly tends to remain adjacent to the protoplasm. Our layer has the same features as this outer non-cellulosic layer of the intine as it easily takes ruthenium stain, swells during chlorination, bulges at the apertures and does not resist acetolysis. On the other hand it is, in contradistinction to the intine, easily stained with basic fuchsin. With ruthenium it is not stained as easily and distinctly as the intine proper. Its separation from the intine suggests that it is not part of it. It is not elastic and easily ruptured at the colpi whereas the intine tends to remain adjacent to the protoplasm in the expanded grains. Its destruction by acetolysis, its stainability with ruthenium red and its thickness at the colpi, are not in favour of a supposed nexinous nature.

With regard to the third suggestion, it is evident that it shares characteristics with the exine as well as with the intine. It protects the protoplasm in apertural regions, which is more of an "exinous" function, and it seems to facilitate the emergence of the pollen tube, which is an "intinous" function. The layer has also been observed in sections of pollen grains of *Durandea angustifolia*, *Hebepetalum humiriifolium*, *Ochthocosmus candidus* (all linaceous plants with tricolpate pollen grains), as well as in thin sections of *Sesamum indicum* (Pedaliaceae; in this species the sporoderm stratification is of much the same type as in *Linum*). The mesine is considered by Rowley to correspond to the endonexine of Erdtman, which in my opinion is not correct, since the endonexine of Erdtman is usually thin and highly refractile whereas the mesine is a lamellated, thick, non-refracting layer. Then the "mesine" is thickened under the apertures forming thick lens-shaped bodies. The latter can probably not be endonexinous as they usually resist acetolysis, etc. In *Clivia miniata* Afzelius (1955) found that the extra-intinous part of the sporoderm is formed by two main layers: an outer acetolysis-proof layer and an inner not acetolysis-proof. She also mentioned that in non-acetolyzed pollen grains a lamellated fine structure had been observed in the latter. Thus the mesine of Rowley and Ehrlich and

the inner layer of the nexine described by Afzelius are of much the same character as the "intermediate" layer in *Linum*.

The question now arises as to whether this layer shall be termed "exintine", "mesine", or maybe "medine". An answer to this question had better be deferred until comprehensive investigations of a wide range of plants have been completed. If in future such investigations prove that there is a definite third layer between intine and exine, I am inclined to call it medine (term suggested by Erdtman). This because "mesine" (Rowley) denotes a layer corresponding to the endonexine of Erdtman and can easily be confused with Fitting's "mesosporium", which, if shortened, becomes "mesine". The word medine (from L. medius) reflects the meaning of a layer between the exine and the intine. This layer may possibly represent a "primitive" layer in the pollen wall. In certain types of colpi it may serve as a protective layer (in addition to the thin exine) and facilitate the emergence of the pollen tube.

The species studied in this work exhibit two main types of apertures, colpi and pores.

From the primitive type of colpus found in *L. austriacum* and *L. perenne*, where the colpi exist as broad, thin, exinous areas, the first line of development is towards the formation of a narrow slit or groove in the sexine (*L. flavum*, *L. bulgaricum*, cf. Tab. 1). In *L. alpinum* the colpi have a short longitudinal slit. This probably represents a transitional stage between the colpus types in *L. flavum* and *L. bulgaricum*. The second line of development is towards the formation of colpi consisting of narrow longitudinal thin exinous areas as in most *Linum* species. The third line is towards the formation of pantoporate pollen grains (*L. rigidum*, *L. multicaule*). The dodecatreme pollen grains of *L. monogynum* and *L. jamaicense* represent transitional stages between tricolpate and the pantoporate grains. Such a line of development is not uncommon in the angiosperms (cf. Takhtajan 1959).

The heterostylous species in *Linum* have dimorphic pollen grains: grains with one kind of processes are produced by brevistylous, grains with processes of two different sizes by longistylous individuals. The homostylous species have pollen grains with monomorphic processes (Laibach 1928). Pollen grains with "heteromorphic" processes (Tab. 1) seem to form an intermediate stage between grains with monomorphic and grains with dimorphic processes.

Table 1.

Species	Pollen size (μ)	Processes	
		Number of shapes	Length \times diam. (μ)
I. Colpate			
A. Tricolpate			
a. Colpus broad, covered			
<i>L. angustifolium</i> Huds., cult. Stockh. (Eur., N. Afr.)	55 \times 48	2	1 \times 2
<i>L. austriacum</i> L., cult. Uppsala (E. Eur.)	65 \times 52	1, 2	2.0, 1.5 \times 3.0, 1.5
<i>L. bienne</i> Mill. Gard., cult. Uppsala (Yugoslavia)	56 \times 46	2	1.0 \times 1.0, 0.5
<i>L. perenne</i> L., cult. Stockh. (Eur.)	65 \times 52	2	2.0, 1.5 \times 3.0, 1.5
b. Colpus broad, covered, with slit.			
<i>L. alpinum</i> L., cult. Edinb. (Eur., N. Afr.)	70 \times 60	1	1.5 \times 2.0
<i>L. betseliense</i> Baker, Straka 143 (Madagascar)	55 \times 46	1	1.5 \times 2.0
c. Colpus, narrow, covered.			
<i>L. catharticum</i> L., Herb. Stockh. (Eur., Orient)	45 \times 40	1	1.5 \times 1.0
<i>L. hirsutum</i> L., Petrak 1494 (Asia Minor)	55 \times 53	> 2	1.5 \times 1.5
<i>L. hologynum</i> Reichb., cult. Edinb. (Thailand)	80 \times 62	1	2.0 \times 1.5
<i>L. komarovii</i> Juz., Gelman s.n. (E. Siberia)	70 \times 60	1	1.5 \times 2.0
<i>L. lanuginosum</i> Juz., Herb. Leningrad (Crimea)	55 \times 45	1	1.0 \times 1.0
<i>L. lewsii</i> Pursh, Centry 2230 (Eur.)	80 \times 67	2	1.5 \times 1.0, 2.0
<i>L. macrorhizum</i> Juz., Gontscharow 662 (C. Asia)	73 \times 60	1	1.5 \times 1.5
<i>L. mumbyanum</i> Boiss., Reute s.n. (Algeria)	45 \times 50	> 2	3.0 \times 3.0
<i>L. nodiflorum</i> L., Herb. Copenhagen (S. Eur.)	60 \times 50	1	2.0 \times 1.5
<i>L. oligophyllum</i> Willd., Pennell 14340 (S. America)	60 \times 60	2	1.5 \times 2.5, 1.0
<i>L. rupestre</i> Engelm., Palmer 149 (N. America)	70 \times 60	2	1.0 \times 2.0, 1.0
<i>L. salsoloides</i> Lam., de Lavernelle s.n. (France)	55 \times 40	> 2	2.0 \times 3.0, 1.0
<i>L. schiedeana</i> Cham., von Türckheim 659 (Mexico)	55 \times 46	1	0.5 \times 1.0
<i>L. selaginoides</i> Lam., Drummond 37 (Argentina)	43 \times 34	1	1.5 \times 2.0
<i>L. setaceum</i> Brot., Welwitsch s.n. (W. Mediter.)	55 \times 50	1	1.0 \times 1.0
<i>L. strictum</i> L., Rechinger 295 (E. Mediter.)	55 \times 47	> 2	2.0 \times 2.0

(Table 1, cont.)

Species	Pollen size (μ)	Processes	
		Number of shapes	Length \times diam. (μ)
<i>L. tenuifolium</i> L., cult. Uppsala (Asia Minor)	58 \times 51	1	1.5 \times 2.0
<i>L. thesioides</i> Bartl., Ecklon and Zeyher 270 (S. Afr.)	50 \times 50	>2	3.0 \times 2.0
<i>L. thunbergii</i> Eckl., Schlechter 6652 (S. Afr.)	56 \times 45	1	1.0 \times 1.5
<i>L. usitatissimum</i> L., cult. Uppsala (E. Eur.)	56 \times 48	1	1.0 \times 1.5
<i>L. viscosum</i> L., Rivas s.n. (S. Eur.)	56 \times 60	>2	1.5 \times 1.5
d. Colpus narrow, uncovered, slit.			
<i>L. adenophyllum</i> A. Gray, Brandege s.n. (Calif.)	54 \times 50	1	1.0 \times 1.0
<i>L. breweri</i> A. Gray, Brandege, s.n. (Calif.)	65 \times 60	1	1.0 \times 0.5
<i>L. bulgaricum</i> Podp., (longistyl.), cult. Uppsala (Eur.)	60 \times 50	2	3.0 \times 2.0, 1.0
<i>L. californicum</i> Benth., Parry 188 (Calif.)	60 \times 52	1	1.0 \times 0.5
<i>L. extraaxillare</i> Kit., (longistyl.) cult. Uppsala, (Thailand)	68 \times 50	2	1.0 \times 2.0, 1.0
<i>L. flavum</i> L., (brevistyl.), cult. Uppsala (S. Eur.)	62 \times 55	1	1.5 \times 1.5
<i>L. grandiflorum</i> Desf., cult. Uppsala (Algeria)	78 \times 62	1, 2	1.5 \times 3.0, 1.5
<i>L. micranthum</i> A. Gray, Hall 9917 (Calif.)	40 \times 35	1	1.0 \times 0.5
<i>L. narbonense</i> L., Erdtman s.n. (S. Eur.)	75 \times 67	2	1.5 \times 2.0
<i>L. olympicum</i> Boiss., Boissier s.n. (Asia Minor)	60 \times 50	>2	2.0 \times 2.0
B. Pantocolpate			
<i>L. jamaicense</i> Fawcett, Harris 12243 (Jamaica)	50 \times 50	1	1.0 \times 1.0
<i>L. monogyne</i> Forst., Carse s.n. (N. Zealand)	70 \times 70	1	1.0 \times 2.0
II. Pantoporate			
<i>L. heterosepalum</i> Regel, Brotherus 192 (Turkestan)	70 \times 70	2	4.0 \times 4.0, 2.0
<i>L. multicaule</i> Hook., Drushel 8340 (N. Amer.)	100 \times 100	2	3.0 \times 4.0, 2.0
<i>L. olgae</i> Juz., Herb. Leningrad (Turkestan)	90 \times 90	2	3.0 \times 4.0, 2.0
<i>L. rigidum</i> Pursh, Macoun s.n. (N. Amer.)	125 \times 125	2	3.0 \times 2.5, 1.5
<i>L. stelleroides</i> Planch., Mazzetti 12583 (China)	70 \times 70	2	1.0 \times 2.0, 1.0

With regard to the geographical distribution (cf. Tab. 1) the following remarks can be made:

"Primitive species" (e.g. *Linum perenne*, *L. austriacum* and *L. angustifolium*) are confined to Europe and North Africa. "Advanced species" with pantoporate pollen grains are found in North-West America, China and Turkestan. Species with pantocolpate pollen grains (*L. monogynum* and *L. jamaicense*) are confined to New Zealand and Jamaica respectively. Species with tegillate sexine are mostly confined to America (*L. breweri*, *L. californicum*, *L. micranthum*, *L. schiedeanum*).

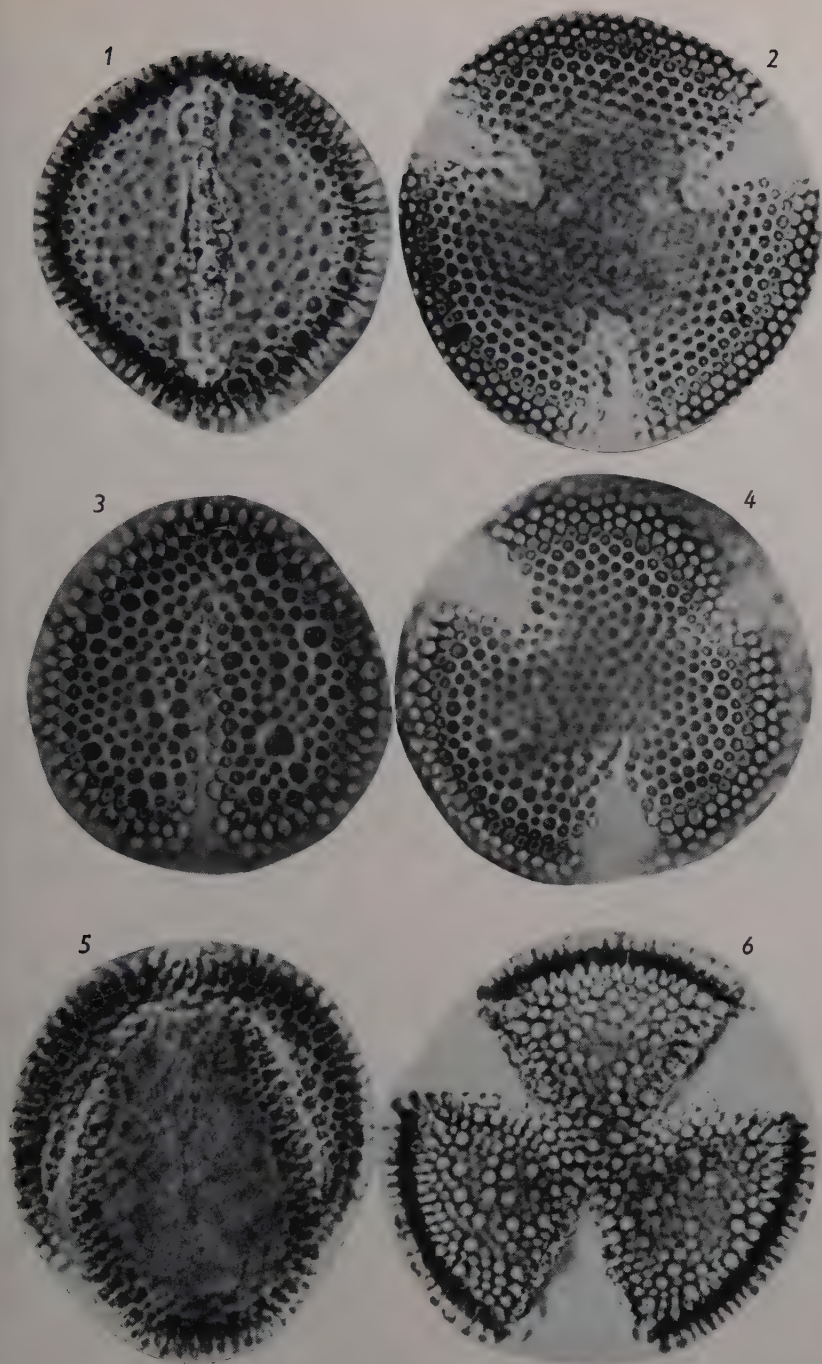
As to the taxonomic classification of the genus *Linum*, Winkler (in Engler and Prantl, Nat. Pfl.-fam., 2nd Ed., Vol. 19 a, 1931) enumerates five sections, viz. Eulinum, Linastrum, Cathartolinum, Syllinum and Cliococca.

Cliococca has only one species, *L. selaginoides*, characterized by sepals longer than petals. Syllinum comprises about 20 species, of which *L. nodiflorum* and *L. flavum* have been studied in connection with the present paper. Before the opening of the flowers the petals are united. Cathartolinum comprises about 50 species characterised, i.a., by sepals with distinct nerves extended right up to the margins of the sepals. Of these species the pollen morphology in *L. multicaule*, *L. rigidum*, *L. rupestre* and *L. schiedeanum* has been studied. Linastrum comprises about 30 species with yellow petals (the pollen grains in *L. mumbyanum*, *L. sectaceum*, *L. thesioides* and *L. thunbergii* have been investigated). Eulinum, finally, comprises the rest of the species. It differs from Linastrum by having larger, blue, pink or white flowers.

With regard to pollen morphology *Linum* can be subdivided in two groups, one with colpate, one with porate pollen grains. The former comprises the "Pantocolpateae" (*L. jamaicense* and *L. monogynum*) and "Tricolpateae" (which can be subdivided into a number of minor groups according to the colpus type as shown in Tab. 1).

The second group (species with porate pollen grains) can possibly be subdivided according to the type of processes covering the pores, etc.

The genus *Linum* with its great variety of pollen patterns can well be regarded, as Hallier (1921) did, as a stock from which a considerable number of families have evolved.



Figs. 1, 2, *Linum austriacum*; 1, equatorial view; 2, polar view showing margins of ruptured colpi. Figs. 3, 4, *L. hirsutum*; 3, equatorial view; 4, polar view. Figs. 5, 6, *L. bulgaricum*; 5, oblique equatorial view showing slit colpi; 6, polar view showing straight colpi margins. — $\times 1000$.

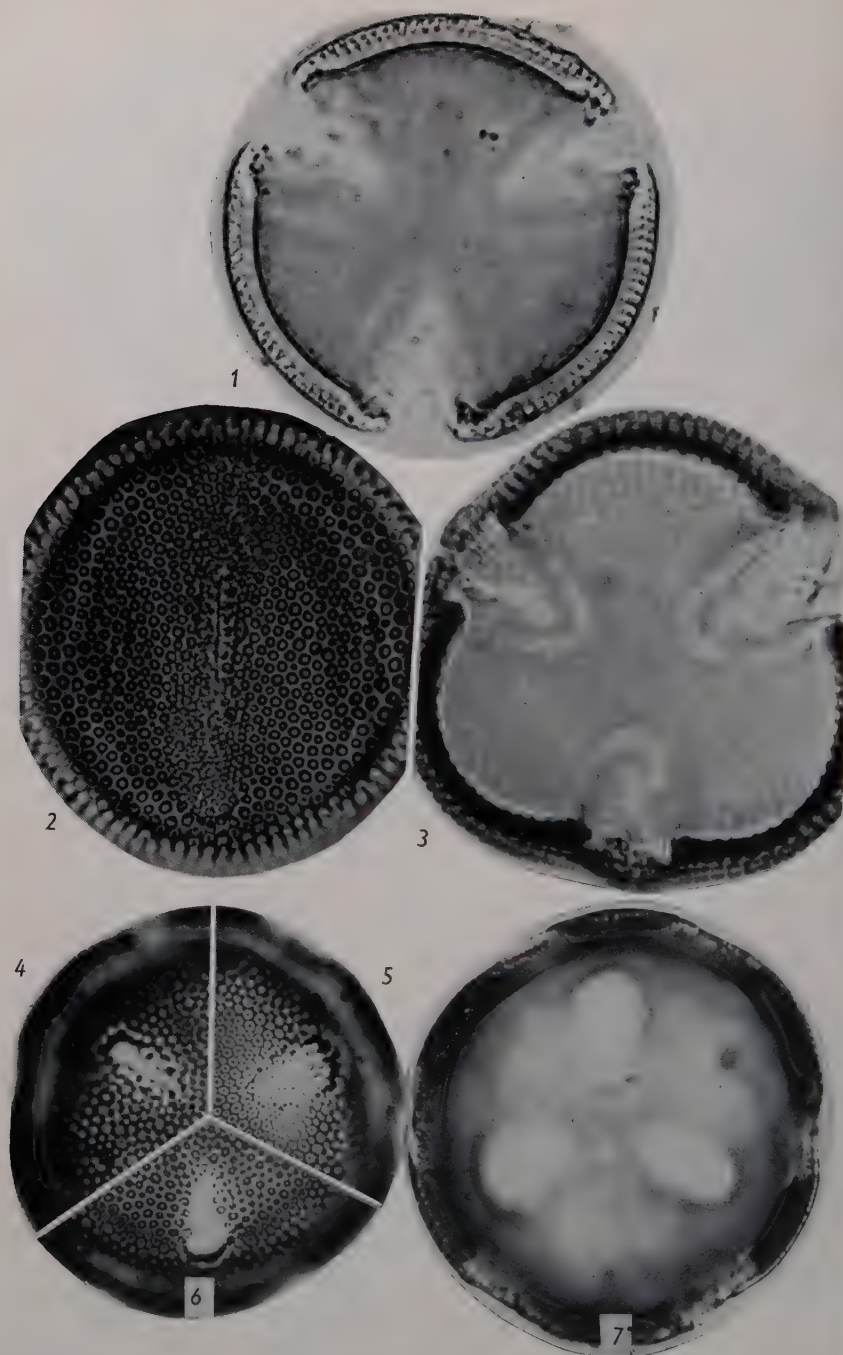
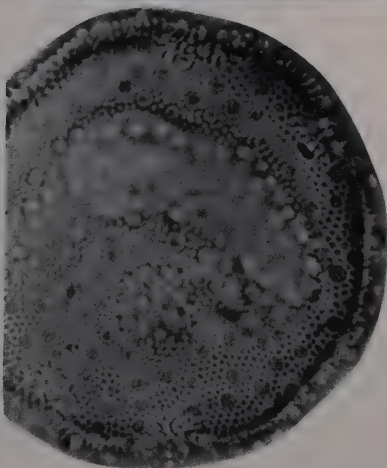
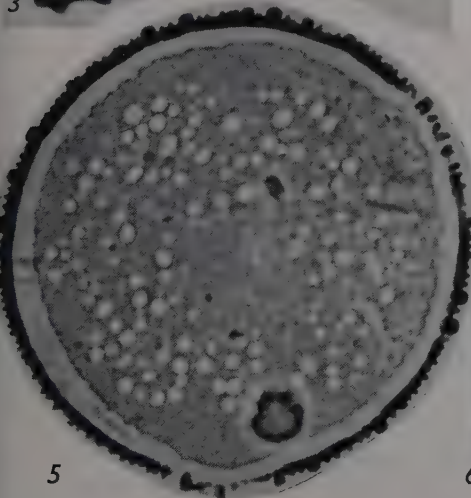
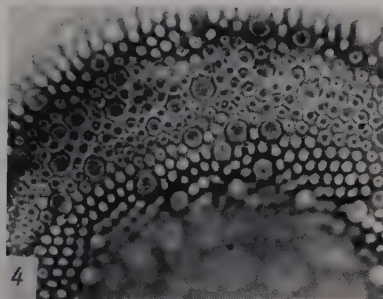
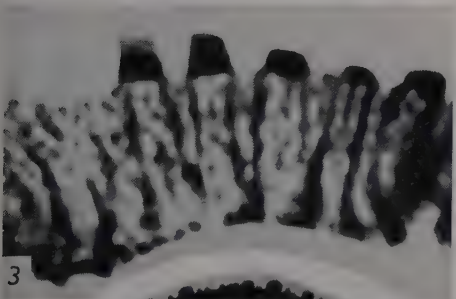
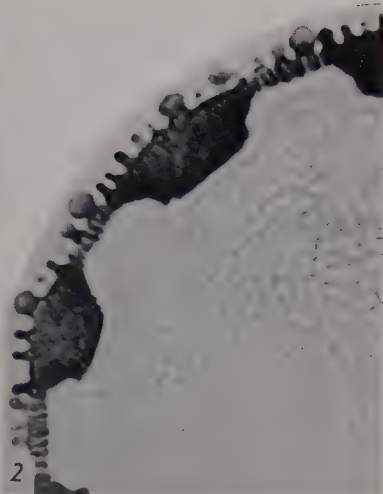
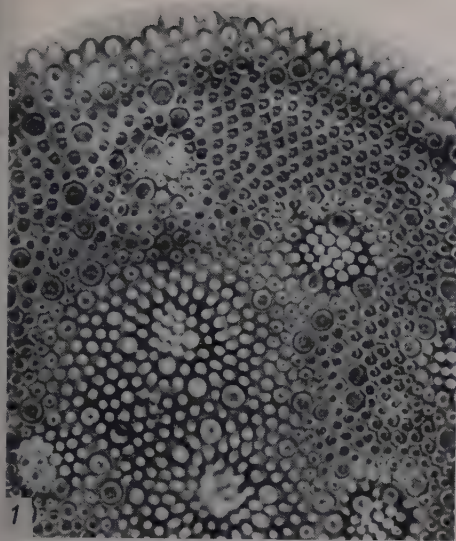


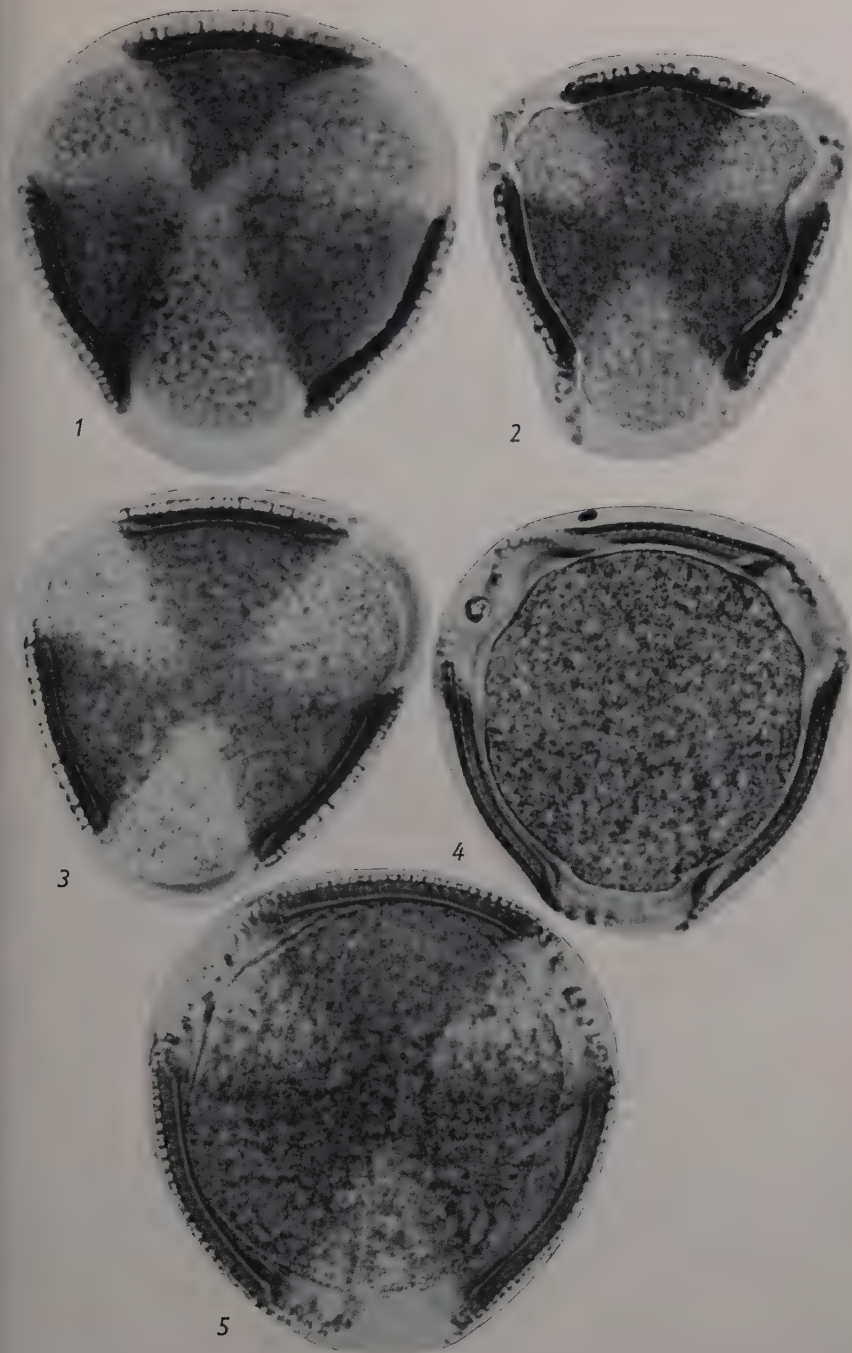
Fig. 1, *Linum austriacum*; acetolyzed pollen grain (optical section) in polar view. Figs. 2, 3, *L. alpinum*; 2, grain showing short colpus slit; 3, optical section of pollen grain in polar view showing a slit in the upper left colpus. Figs. 4-7, *L. monogynum*; 4-6, Lo-patterns of the exine; 7, optical section. $\times 1000$.



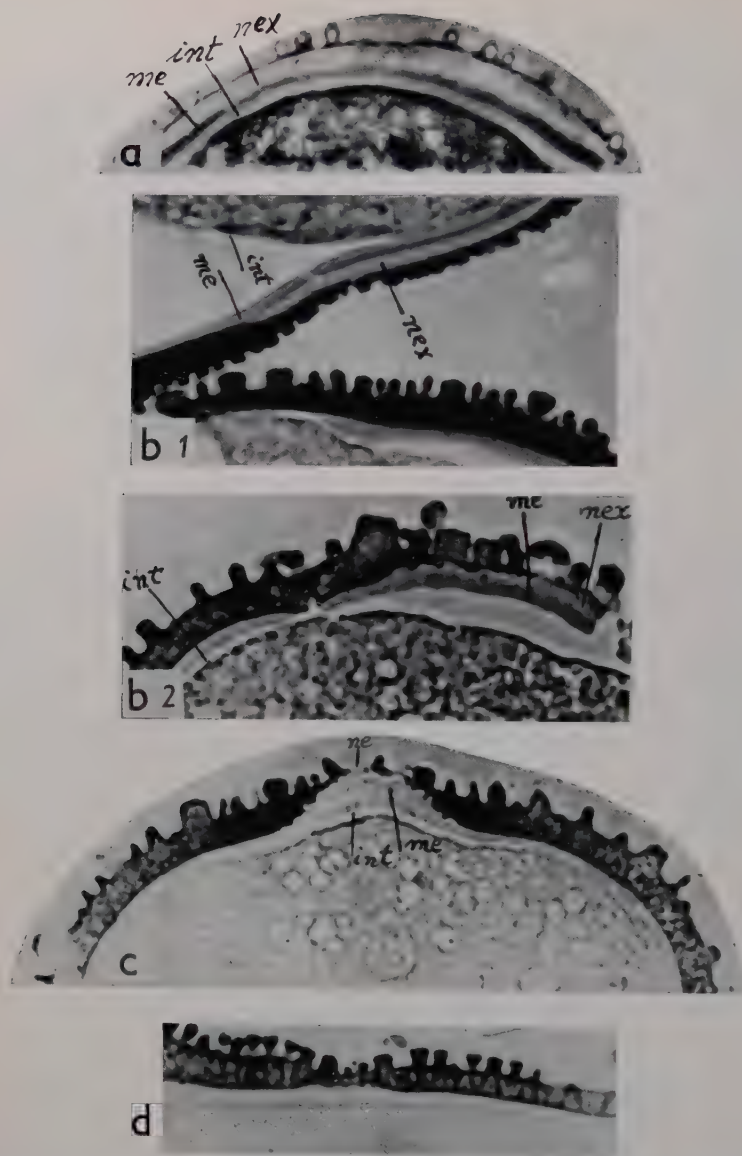
Figs. 1, 2, *Linum rigidum*; 1, part of pollen grain with sexinous processes covering, i.e., the pores ($\times 850$); 2, part of section through an unacetolyzed pollen grain stained with fuchsin (pores covered with bacularia), $\times 1000$. Figs. 3, 4, *L. multicaule*; 3, part of section through the exine of an acetolyzed grain showing baculoid elements, $\times 3000$. 4, part of grain showing cryptopores, $\times 1000$. Figs. 5, 6, *L. stelleroides*; 5, section through an unacetolyzed grain showing pores studded with free baculoid elements; 6, part of grain showing cryptopores, $\times 850$.



Figs. 1-4, *Linum grandiflorum*; 1-3, LxO-patterns; in 1 the small processes amalgamated to form the bigger ones can be seen; 4, optical section showing sexine and nexine ($\times 900$). Figs. 5-7, *Linum catharticum*, LxO-patterns; sexinous processes all monomorphic ($\times 1000$). Fig. 8, *Linum hirsutum*, showing heteromorphic processes ($\times 1000$).

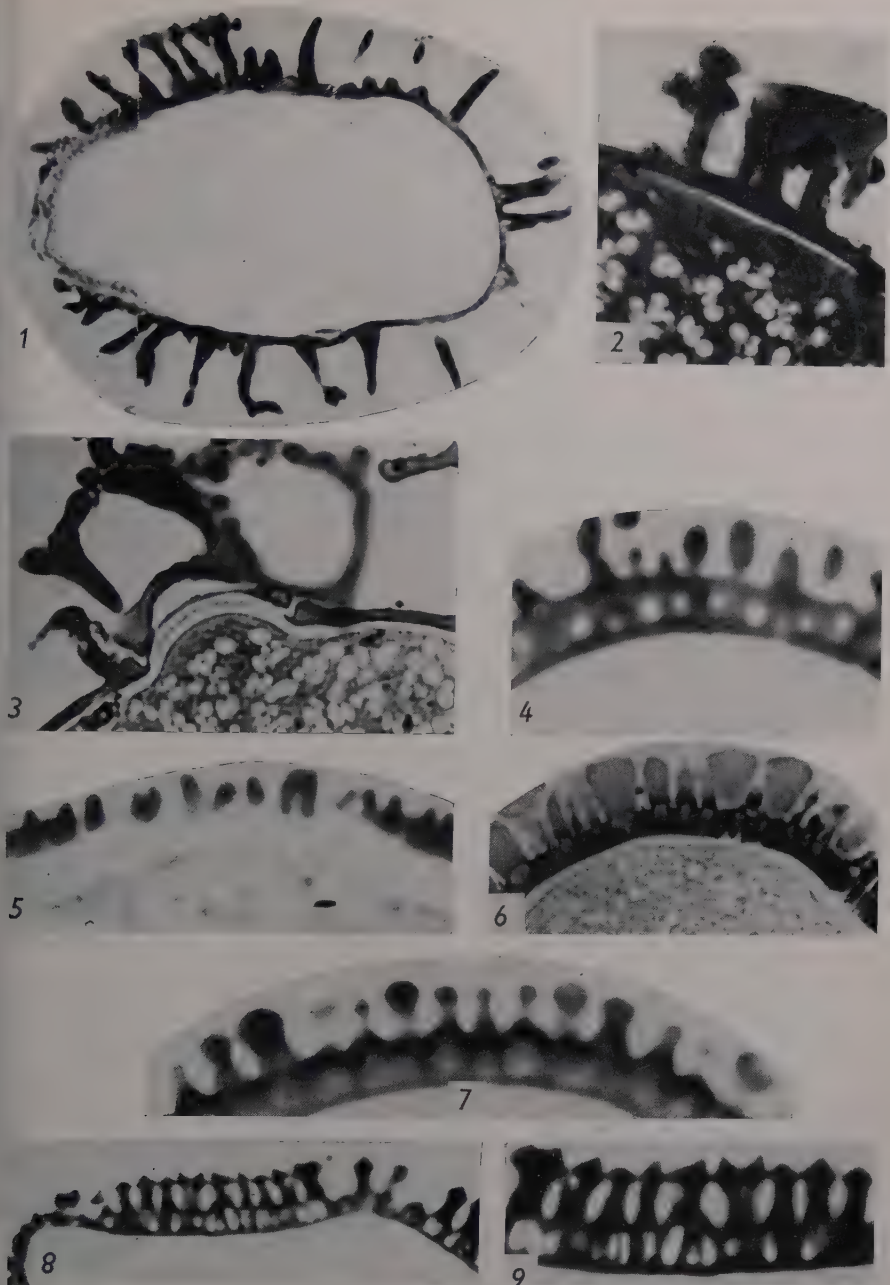


Chlorinated pollen grains stained with ruthenium red. Fig. 1, *Linum flavum*. Fig. 2, *L. bulgaricum*. Fig. 3, *L. austriacum*. Fig. 4, *L. perenne*. Fig. 5, *L. alpinum*. $\times 1000$.



Sporoderm sections. Figs. a, b₁, b₂, *Linum angustifolium*, un-acetolyzed grains stained with fuchsin ($\times 1500$; a, apertural region). Fig. c, *Linum perenne* ($\times 1200$). Fig. d, *L. bulgaricum* (baculoid elements in "granular" sexine ($\times 1200$). Int.: cf. intine; med: cf. medine; nex.: cf. nexine).

Fig. 1, *Limonium tubiflorum*; section showing bacula rooted in the nexine (right), tegillate sexine (top left) and granular colpus membrane (left). Figs. 2, 3, *Cobaea scandens*; sections showing thick nexine and thick bacula united at top to form a tegillum. Fig. 4, *Linum catharticum*; section through acetolyzed exine showing nexine, bacula, tegillum, and suprattegillar processes ($\times 3500$). Fig. 5, *Linum stelleroides*; pore filled with free baculoid elements ($\times 3000$). Fig. 6, *Reinwardtia tetragyna*; pores filled with bacularia; exine, processes excepted, mainly formed by bacula separated by a granular matrix. Fig. 7, *Linum flavum*; section through acetolyzed exine showing processes and, within the main part of the exine, baculoid elements ($\times 3000$). Figs. 8, 9, *Hugonia tomentosa*; exine mainly consisting of bacularia (8: $\times 1500$; 9: $\times 3000$).



For explanation, see Pl. VI, lines 1-10 from below.

Summary

1. In the present study the pollen morphology and sporoderm stratification in 44 species of *Linum* have been considered.

2. Evolutionary tendencies: (a) increase in size of the pollen grains; (b) progress from a tricolpate to a pantoporate apertural status; (c) sexinous processes tending to be dimorphic; (d) sexine showing a transition from a "primitive" granular state to the formation of a tegillum supported by bacula (see also Addendum, p. 126).

3. New types of colpi as well as pores ("cryptopores" and "hemicyptopores") have been described.

4. The sexine consists of granular elements which often seem to form a complicated three-dimensional network. It is surmounted by processes which are a continuation of the main sexine layer. Due to "condensation" of the sexine granules more or less baculoid rods are formed. The nexine is relatively thin and no granulation has been seen in it except at the apertures (cf. also Addendum).

5. In the species with colpate pollen grains a special layer, "medine", situated between the intine and nexine, has been noticed. It is easily stained by fuchsin and by ruthenium red. It does not resist acetolysis and often separates from the intine during sectioning. It bulges at the colpi forming lens-shaped layers. It sometimes shows lamellation.

6. Pollen characters should be duly considered in a reclassification of the genus. *Linum* is palynologically a very interesting and important genus, and the Linaceae probably form a stock from which many other genera and families may have been evolved.

Acknowledgements

I wish to express my gratitude to the Swedish Institute for a grant by which the above investigation was made possible. The investigation was carried out at the Palynological Laboratory of the Swedish Natural Science Research Council, Stockholm-Solna. I am indebted to Professor G. Erdtman for putting the material and the facilities of the Palynological Laboratory at my disposal. Thanks are also due to Mr. R. Praglowski for his great help in preparing the photomicrographs and to the Directors and Keepers of the Botanical Gardens and Herbaria where the material for the investigations was gathered.

Addendum

A TENTATIVE OUTLINE OF SOME TRENDS IN THE PHYLOGENETIC DEVELOPMENT OF EXINE STRATIFICATION

Linum perenne and *L. grandiflorum* have tricolpate pollen grains with "primitive" colpi (developed as broad thin areas in the exine). Thin sections show that the "sexine" consists of granuloid elements forming a complicated network-like structure (Fig. 2 j-k and Pl. IV: 4, Pl. VI c). These elements are particularly densely packed at the outer- and innermost parts of the "sexine". The nexine proper does not show any granulation except at the colpi where it forms the granular colpus membranes.

Linum bulgaricum and *L. flavum* have a more "advanced" type of colpi. In thin sections it can be seen that sexinous granular elements are locally agglomerated into baculoid structures (Fig. 2 h and 4 e; Pl. VI d and VII: 7). The nexine is thin, structureless, refracting. In the pantoporate pollen grains in *L. heterosepalum* and *L. stelleroides* the apertures are covered with the same kind of processes as the general surface of the exine. Their free baculoid roots abut on the nexine (Pl. VII: 5).

In the supposedly more advanced species of *Linum*, e.g. *L. rigidum* and *L. multicaule*, the sexinous processes have short, free baculoid roots whereas the pores are covered by characteristic bacularia-like processes. Thin sections (Pl. III: 2-3) show that the "sexine" consists of granular elements agglomerated into baculoid structures separated by granular substance with less densely spaced granules. The baculoid structures are connected with the roots of the superficial processes. In *L. multicaule* there is no sharp boundary between nexine and sexine.

In *Reinwardtia tetragyna* Planch. thin sections show that the pores are covered with bacularia-like processes. In the extraporal sexine the same kind of processes are found (Pl. VII: 6); their roots, however, are still connected with the remains of the granular material of the sexine. The nexine is thin, homogenous. Thin sections through the pollen wall of *Hugonia tomentosa* Cav. show that the "sexine" consists of groups of bacularia standing on the nexine (Pl. VII, Figs. 8, 9). No trace of granules could be seen. The granular nature of the nexine is apparent at the colpi where the nexine seems to be divided into two very thin layers forming the colpus membrane.

In *Durandea angustifolia* Stapf sections show that the "sexine"

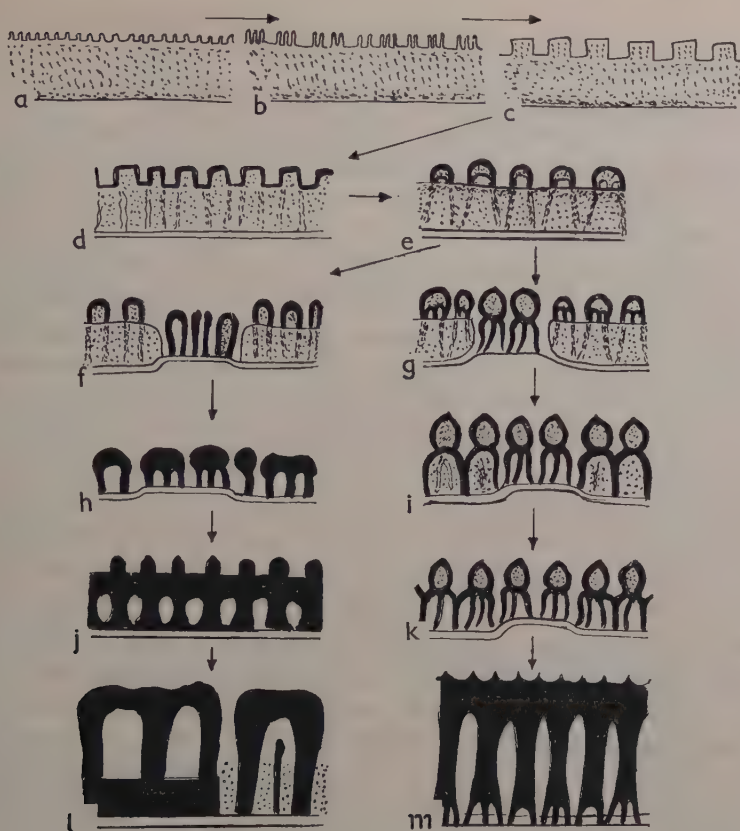


Fig. 4. Diagrammatic representation of phylogenetic trends of development of exine structure in some linaceous, polemoniaceous and plumbaginaceous plants. — a, b, hypothetical pre-stages. — c, d, *Linum perenne* and *L. angustifolium*. — e, *L. bulgaricum*, *L. flavum*. — f, *Anisadenia pubescens*, *L. stelleroides*. — g, *Linum multicaule*, *L. rigidum*. — h, *Durandea angustifolia*. — i, *Reinwardtia trigyna*. — j, *Linum catharticum*. — k, *Hugonia tomentosa*. — l, *Cobaea penduliflora* (right), *C. scandens* (left). — m, *Limonium tubiflorum*.

consists of thin bacula, standing on the structureless nexine. At their top they are united into a reticulate tegillum.

In *Linum catharticum* the sexine consists of thick baculoid rods united at the top to form a tegillum with suprategillar processes (Pl. VII: 4).

In some pollen types with sexinous processes amalgamation of granules at the surface of the exine has led to the formation of small processes. These processes may unite to form bigger ones, which still retain their granular nature in the centre, although they are surrounded by a non-granular hyaline layer. LO-analyses of the exine

show that the degree of amalgamation varies in different species. Thus the units forming the bigger processes can be seen as a number of small bright dots at the top of the processes (Fig. 3). In some species these units can be traced along the whole extent of the processes. In the pollen grains in certain plumbaginaceous genera, e.g. *Plumbago* and *Ceratostigma*, the small processes which unite to form the bigger ones, are very distinct.

Two evolutionary lines in exine development are diagrammatically represented in Fig. 4. The first line leads to the features encountered in *Reinwardtia*, *Hugonia*, *Plumbago*, and *Ceratostigma*. The second line points towards the formation of separate bacula (as those in the pores of *Anisadenia* and *Linum stelleroides*). In *Durandea* the whole sexine is formed of such bacula which unite at the top and form a reticulate tegillum. For *Linum catharticum*, see above.

In *Cobaea penduliflora* Hook. the exine is formed of granular elements (cf. Erdtman 1952, Fig. 193, p. 330). Bacula-like, non-granular rods are standing on its basal layer. They later unite at the top to form a reticulate tegillum. In *Cobaea scandens* Cav. there is a solid structureless nexine without traces of "roots" of the superimposed sexinous bacula (Pl. VII: 2, 3; J. Praglowski sect. and phot.).

In *Limonium* and *Armeria* the sexine exhibits long baculoid thick rods merging, by way of short "roots", with the nexine. In their upper part they are united to form a reticulate tegillum beset with small spinules (Pl. VII: 1). These rods are similar to the bacularia met with in *Hugonia*, *Plumbago* and *Ceratostigma* although their roots are much shorter. Probably the granular exine structure, dominating in "primitive" types, diminished in relatively "advanced" species and disappeared in the more advanced ones.

The present addendum emphasizes, i.a., the difficulties sometimes met with in drawing a sharp line of demarcation between "tectate" and "intectate" pollen grains. Further investigations are necessary to elucidate the occurrence of "endogeneous" bacula and the phylogenetic importance of the series: uniformly granulate exine → exine with granules locally agglomerated to form baculoid streaks → baculate, tegillate exine (with or without suprattegillar processes).

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MORPHOLOGY OF NORMAL AND SOME ABNORMAL POLLEN GRAINS OF *PINUS ROXBURGHII* SARG.

BY

S. K. SRIVASTAVA

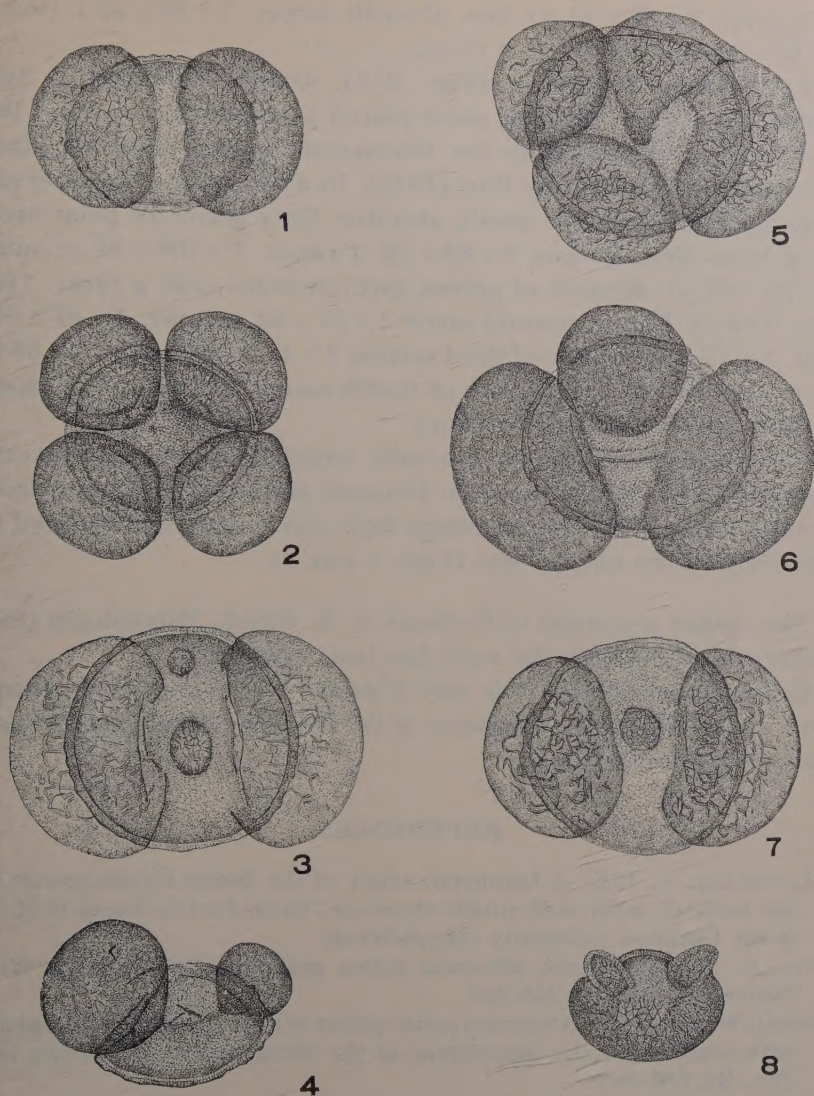
The pollen grains of *Pinus roxburghii* Sarg. usually have a body with two airsacs of more or less equal size. Generally, any deviation in the number of sacci has been taken as an abnormal form. Earlier, Chatterjee (1943) observed a few abnormal pollen grains of *Pinus longifolia* Roxb. (*Pinus roxburghii* Sarg.) with two to three sacci. Vishnu Mittre (1957) has further noted abnormal grains with one to four sacci. In the present study di-, tri-, and tetrasaccate pollen grains are reported with many intermediate stages.

The material comes from trees in the outskirts of Dehra Dun. The slides were prepared by the acetolysis method. The measurements given are means of at least ten grains measured.

42,000 pollen grains were counted, of which 0.18% were abnormal. Among the latter, 16% were tetrasaccate, 48% trisaccate and 36% disaccate.

Normal disaccate grains (Fig. 1). Corpus rounded in polar view, rounded triangular in equatorial view, $56 \times 83 \times 68 \mu$ (maximum size $78 \times 105 \times 83 \mu$; minimum size $40 \times 63 \times 50 \mu$). Breadth of grains, sacci included, 120μ (max. 160, min. 88μ). Size of sacci: $48 \times 73 \times 58 \mu$ (max. $70 \times 93 \times 90 \mu$; min. $35 \times 58 \times 43 \mu$).

Trisaccate grains (Figs. 5-7). Corpus rounded, provided with two large sacci and a third smaller one. Only grains in polar view have been seen. Corpus $? \times 87 \times 78 \mu$ (max. $? \times 105 \times 90 \mu$; min. $? \times 70 \times 55 \mu$). Breadth of grains, sacci included, 144μ (max. 155, min. 118μ). Size of large sacci: $? \times 80 \times 54 \mu$ (max. $? \times 104 \times$



Figs. 1-8. Camera lucida sketches of normal and abnormal pollen grains in *Pinus roxburghii* Sarg. $\times 250$.

1: Normal disaccate grain. — 2: Tetrasaccate grain. — 3: Tetrasaccate grain; two sacchi are rudimentary. — 4: Disaccate grain; one saccus is much smaller than the other. — 5: Trisaccate grain; one saccus bilobed. — 6: Trisaccate grain. — 7: Trisaccate grain; one saccus rudimentary. — 8: Disaccate grain; both sacchi rudimentary.

71 μ ; min. ? \times 59 \times 41 μ). Size of small saccus: ? \times 39 \times 33 μ (max. ? \times 63 \times 55 μ ; min. ? \times 15 \times 15 μ).

Tetrasaccate grains (Figs. 2-3). Corpus rounded. A few pollen grains have all four sacchi placed symmetrically around the body; they are similar to the tetrasaccate pollen grain of *Pinus excelsa* Wall. recorded by Puri (1945). In a few grains two sacchi are large and the other two small, abortive. Only grains in polar view have been seen. Corpus ? \times 86 \times 78 μ (max. ? \times 100 \times 95 μ ; min. ? \times 73 \times 65 μ). Breadth of grains, sacchi included, 132 μ (max. 145, min. 115 μ). Size of normal sacchi: ? \times 77 \times 53 μ (max. ? \times 97 \times 65, min. ? \times 55 \times 45 μ); size of third saccus: ? \times 45 \times 38 μ (max. ? \times 68 \times 58 μ ; min. ? \times 20 \times 15 μ); size of fourth saccus: ? \times 28 \times 28 μ (max. ? \times 55 \times 48 μ ; min. ? \times 10 \times 10 μ).

The trisaccate grains are generally larger than normal disaccate and tetrasaccate grains. In some disaccate grains one of the two sacchi is much reduced in size; in others both sacchi have been reduced to a fraction of the normal size (Figs. 4 and 8).

The author is grateful to Professor A. K. Ghosh, Palynologist (Sr), under whose guidance the work has been completed.

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